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SOME HETEROBASIDIOMYCETES FROM EASTERN CANADA

G. W. MARTIN

(WITH 9 FIGURES)

Collections made during recent years in the provinces of Ontario and Quebec by Professor H. S. Jackson and students, and by his associate, Dr. R. F. Cain, have brought to light a considerable number of Heterobasidiomycetes. Many of these have been sent to me annually for identification. A selected number, recognized by Professor Jackson as of special interest, were allowed to accumulate and finally sent to me in one lot in the fall of 1939 with the request that they be critically studied and such of them as seemed worthy of record be included in a special paper. The present report is the result of the study of these collections. Among them several seem to be undescribed; others either have not as yet been reported from North America or for other reasons appear to justify discussion and illustration. Of the latter group, only one is here discussed. Since several of the species proposed as new were recognized by Professor Jackson as probably undescribed, he has consented to join me in the authorship of certain of them. The joint authorship is indicated following the specific name in each such case. All the collections mentioned are deposited in the herbarium of the University of Toronto and many of them are also in the collections of the University of Iowa. Unless otherwise stated all collections were made by H. S. Jackson.

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Sebacina (Bourdopia) rimosa Jackson & Martin, sp. nov.
(FIG. 1)

Late effusa, floccoso-rimosa, margine indeterminata, ex pallida ad atromelleam; hyphae nodoso-septatae, $1.5-2\ \mu$, gloeocystidia et basidia gerentes; gloeocystidia clavata, primum hyalina demum flava; probasidiis globosis vel ovatis, usque ad $16\ \mu$ diam., dein cruciato-septatis; basidiosporis subglobosis vel cylindricatis, $12-13 \times 8.5-9\ \mu$, per repetitionem germinantibus.

Broadly effused, floccose-rimose, with indeterminate margin; pallid to citrine drab (R) * not greatly altered when soaked; in section $35-70\ \mu$ thick, composed of a thin mycelial layer parallel with the substratum consisting of hyphae $1.5-2\ \mu$ in diameter, with frequent clamp connections, giving rise directly to gloeocystidia and to hyphae which bear both gloeocystidia and basidia; gloeocystidia clavate, often with broad, furcate base, at first colorless, then filled with yellow, amorphous material, $15-35 \times 5-7.5\ \mu$; probasidia globose or broadly ovate, up to $16\ \mu$ in diameter, becoming longitudinally septate into two or four cells, the cells exhibiting a tendency to separate at the apex; epibasidia rather short, rarely exceeding the hypobasidium, the mature basidia somewhat urniform; basidiospores varying from subglobose to short cylindrical, but mostly broadly ovate, $12-13 \times 8.5-9\ \mu$, germinating by repetition or by the production of a diploid mycelium.

ONTARIO: Maple, Nov. 13, 1938. On *Thuja occidentalis*. U. of Tor. 13086. Type.

The lower portion of the hymenium is composed of a nearly continuous layer of colored gloeocystidia; the upper portion of younger, paler, often hyaline gloeocystidia and rather sparsely distributed basidia. Present in every mount are chains of vesicular cells, some filled with homogeneous protoplasm, others empty, but it may be doubted whether these have any connection with the *Sebacina*.

Sebacina (Bourdopia) Pini Jackson & Martin, sp. nov. (FIG. 2)

Effusa, tenua, margine indistincta, sicca cinerea, humescens ceracea, squallide mellea, in sectione $50-120\ \mu$ cr., gloeocystidia primo pallida, demum flava; probasidiis globosis, $22-24\ \mu$ diam., decentibus cruciato-septatis; epibasidiis brevibus; basidiosporis cylindricatis, $19-22 \times 9-10\ \mu$, per repetitionem germinantibus.

Effused, thin, arid, with indeterminate margin, smoke gray (R) with pruinose surface when dry, becoming olive buff (R) and

* (R) indicates use of a color name in the sense of Ridgway.

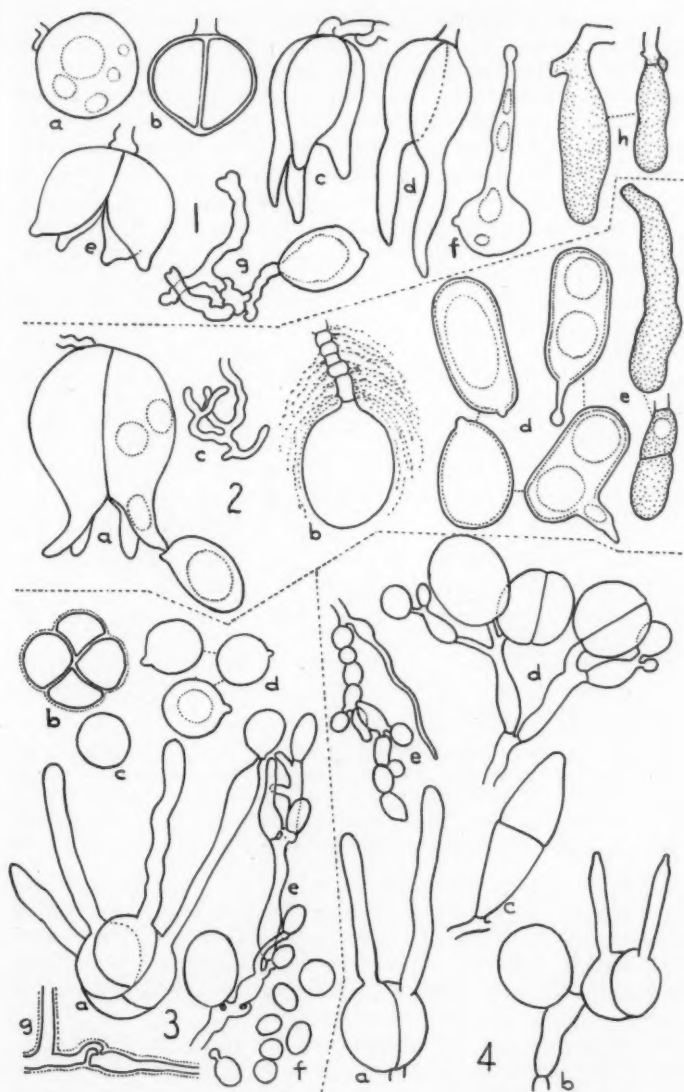


FIG. 1, *Sebacina rimosa*; 2, *S. Pini*; 3, *Tremella mycophaga*; 4, *T. simplex*.

somewhat waxy when soaked, 50–120 μ thick; basal layer scantily developed, the bulk of the fructification composed of a dense mass of gloecystidia and basidium-bearing hyphae; gloecystidia at first hyaline, then yellow, the contents nearly homogeneous, sometimes divided by a transverse septum into two, rarely three cells, 15–45 \times 5–6 μ ; probasidia borne at the surface at the tips of the fertile branches, broadly obovate, then globose, 22–24 μ in diameter, proliferating from the basal clamp connection, becoming cruciate-septate; epibasidia merged with sterigmata, short, divergent, the mature basidium distinctly urniform; paraphyses colorless, much branched at tips, about 1 μ in diameter; basidiospores mostly cylindrical 19–22 \times 9–10 μ but varying to ovate, 16–18 \times 10–11 μ , germinating by repetition.

ONTARIO: Maple, Nov. 6, 1938. On *Pinus Strobus*. U. of Tor. 13090. Type.

Differing from all previously described arid, gloecystidiate species of *Sebacina* in the very large basidia and spores. There are occasional suggestions of the involucre sheath of collapsed basidia (FIG. 2b) characteristic of many species of *Bourdotia* but they are not prominent in the present collection. The fungus occurs in rather long and narrow patches on the substratum, the longest being about 70 \times 5 mm. It is not unlikely that it may occur in much more extensive growths.

***Tremella mycophaga* sp. nov. (FIG. 3)**

Pulvinata, molliter gelatinosa, hyalina vel dilutissime rosea aut ochracea, 0.3–1.5 mm. lata; fructificationibus confluentibus, demum subcerebriformibus; conidiis copiosis, hyphis basidioferis portatis, variabilibus, plurimis 4–7 \times 2.5–4 μ ; probasidiis globosis, 13–15 μ diam., demum cruciatim divis; basidiosporis globosis, 6–8 μ diam., per repetitionem germinantibus.

Fructification pulvinate, discoid, 0.3–1.5 mm. in diameter, larger by confluence, up to 1 cm. or more in extent and then covering several adjacent fructifications of the host, soft gelatinous, hyaline to pinkish or pale yellow-brown when wet, horny, hyaline to dark brown (about warm sepia R.) when dry; surface at first smooth but becoming tuberculate-subcerebriform, partly as a result of confluence, partly by the formation of small tubercles on the individual units; internal hyphae immersed in a soft jelly, slender but irregular, with many vesicular swellings and abundant and conspicuous clamp connections; conidia profuse at all stages, variable in size and shape but mostly subglobose, (2–)4–5(–7) μ in diameter, or

ovate, $4-7 \times 2.5-4 \mu$, germinating by budding; basidia borne on same hyphae as conidia; probasidia globose, $13-15 \mu$ in diameter, readily detached, becoming cruciate-septate; epibasidia up to 50μ in length, $2-3 \mu$ in diameter except toward the tip where they swell to $4-6 \mu$, forming conspicuous apophyses below the slender sterigmata; basidiospores $6-8 \mu$ in diameter, germinating by repetition.

On *Aleurodiscus amorphus* on *Abies balsamea*: Ontario, Quebec, New York.

Specimens examined: ONTARIO: Algonquin Park, Sept. 18, 1938, U. of Tor. 13421. Type; Sept. 15, 1938. U. of Tor. 13420; Sept. 18, 1930, U. of Tor. 13448; Lake Temagami, June 21, 1933, U. of Tor. 6399; July 20, 1935, U. of Tor. 8342; Aug. 19, 1936, U. of Tor. 11063; Aug. 29, 1936, U. of Tor. 11060; Aug. 20, 1937, U. of Tor. 13547. QUEBEC: Ste. Catharine, Aug. 25, 1938, R. F. Cain 11124; Duchesnay, Aug. 25, 1938.

In connection with his study of *Aleurodiscus amorphus*, Stork (Am. Jour. Bot. 7: 447-448. 1920) described and illustrated, but did not name this species. Stork's description was apparently drawn largely from stained microtome sections and was, of course, incidental to the subject matter of his paper. He did note the tendency of the hypobasidial segments to separate. From the study of the Canadian material it seems certain that the segments may become completely separate and round up in spore-like form (FIG. 3b, c) before developing epibasidia, in which case they can be distinguished from basidiospores only by the absence of an apiculus. Dr. Stork has kindly placed his slides at my disposal and there can be no question that his reference is to the present species.

***Tremella simplex* Jackson & Martin, sp. nov. (FIG. 4)**

Pulvinata, molliter gelatinosa, hyalina vel dilutissime rosea aut ochracea, 0.3-1.5 mm. lata; fructificationibus confluentibus, demum subcerebriformibus; conidiis copiosis, hyphis basidioferis portatis, variabilibus, plerumque $4-7 \times 2.5-4 \mu$; probasidiis subglobosis, $10-13 \mu$ diam.; vel fusoidiis et igitur pro portione gracilis, uniseptatis, ex hyphis haud nodosis; basidiosporis subglobosis, $6.5-8 \mu$ diam.

Exactly like *T. mycophaga* in habit, shape, size, color and consistency, and like it, bearing conidia on the same branches as the basidia; differing in the complete lack of clamp connections, the smaller probasidia varying in shape from globose through ellip-

tical to elongate fusoid; in the constantly single septum which, in the shorter basidia may be in any plane with reference to the axis of the basidium, but is usually transverse or nearly so in the longer basidia. The spores are not quite so regularly globose as in *T. mycophaga* but the difference is not great enough to be stressed.

On *Aleurodiscus* sp. on *Thuja occidentalis*, Ontario and Quebec.

Specimens examined: ONTARIO: Lake Temagami, Sept. 4, 1937, U. of Tor. 11650, Type. Same locality, Aug. 13, 1937, U. of Tor. 11653A. QUEBEC: Ste. Catharine, Aug. 25, 1938.

There is a strong temptation to regard this as a haploid variety of *T. mycophaga*. The lack of clamp connections and the constant 2-celled character of the mature basidia together with their smaller size and tendency to greater irregularity of shape and orientation of the septum are exactly what might be expected of a haploid form. Whether this is the case or not can be decided, however, only by cultural studies and cytological comparison. In the meantime the existence of three collections from two rather widely separated localities, all parasitizing an undescribed species of *Aleurodiscus*, which is not the host of *T. mycophaga*, justify designating this form by a distinct name.

PLATYGLOEA PENIOPHORAE Bourd. & Galz. Bull. Soc. Myc. Fr.
25: 17. 1909 (FIG. 5)

A collection on *Tilia* near Maple, Ontario, Oct. 6, 1937 (U. of Tor. 12401), is doubtfully assigned to this species. Another on *Populus*, from Holland River Marsh, May 6, 1936, by R. F. Cain (U. of Tor. 12834) is certainly the same. The former is marked "associated with *Peniophora* sp." but aside from some large spores, clearly not belonging to the *Platyglœa*, and some mycelial fragments, there is little that suggests *Peniophora* in the mounts. Nevertheless, I believe that it is preferable to refer these collections to Bourdot and Galzin's species for the time being rather than to give them a new name.

In the original description no spore size is given. Later Bourdot and Maire (Bull. Soc. Myc. Fr. 36: 69, 1920) reported them as $7-10 \times 4-6 \mu$. Wakefield and Pearson (Trans. British Myc. Soc. 8: 219. 1923) give the measurements as $8-9 \times 5-5.5 \mu$ and note

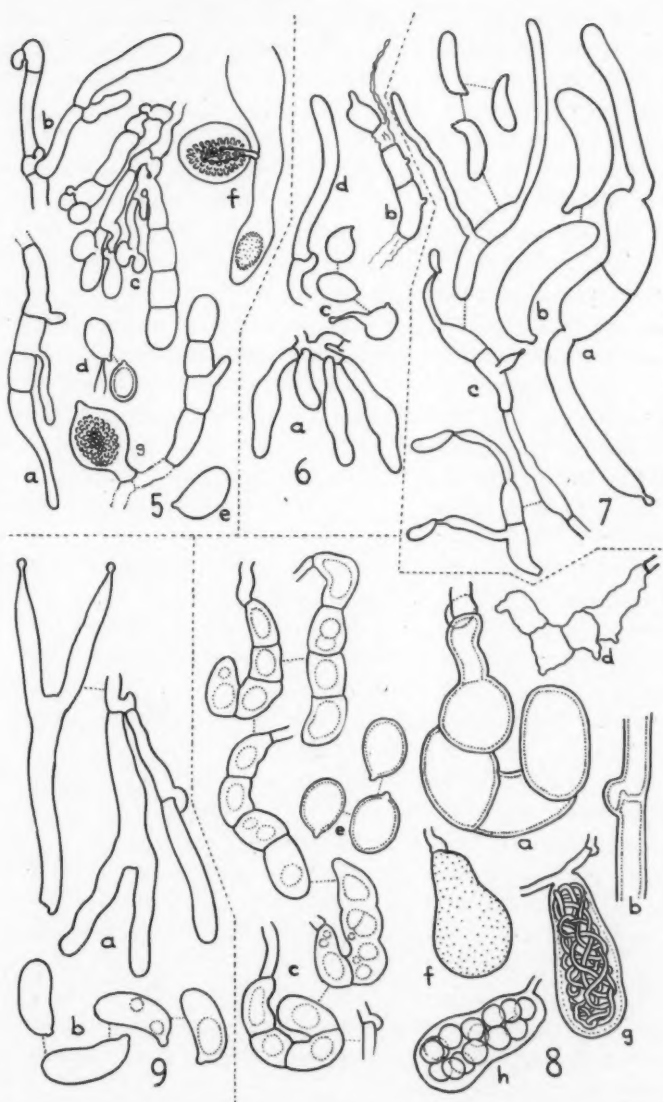


FIG. 5, *Platyglöea Peniophorae*; 6, *P. fusco-atra*; 7, *P. pustulata*; 8, *Helicobasidium candidum*; 9, *Ceracea canadensis*.

that they germinate by repetition. In their final publication Bourdot and Galzin (Hym. France 12. 1928) cite the spore size as $7-8 \times 5-6 \mu$. There are other differences between the various descriptions. Bourdot and Galzin emphasize the horny character when dry. Wakefield and Pearson describe the fungus as not horny but thin, white and markedly pulverulent, with shorter "sterigmata." They attribute the differences, reasonably enough, to the fact that their material was probably younger.

The Canadian collections form rather conspicuous effused white or ochraceous patches over 10 cm. long and 2 cm. wide. The presence of thicker patches, somewhat gelatinous when wet, suggests that the fructifications originate as separate pustules which rather quickly anastomose. A few horny patches are present, but these are either sterile or the *Platyglea* may be growing over the surface of some other fungus, since in both collections the wood is old and rotten, and remnants of various other fungi are present. The delicate tortuous hyphae are well provided with clamp connections and there is a clamp connection at the base of each basidium, which proliferates to form another basidium, so that the groups of basidia tend to occur in loose, one-sided, cymose clusters. Some of the basidia in such clusters fail to develop fully and become transformed into conidiophores which produce irregularly globose, nearly sessile conidia. The basidiospores are ovate, very slightly flattened ventrally and with a small, or rarely large apiculus, mostly $5-7 \times 3.5-4.5 \mu$, but occasionally as large as $8.5 \times 5 \mu$.

In addition to these structures there are present in abundance on both collections curious vesicular cells, borne upon hyphae with clamp connections and sometimes interspersed with the basidia. The contents are at first homogeneous but soon become nearly filled with small oval bodies, about $1.5 \times 1 \mu$. In some cases these seem to surround a central, columella-like stalk. These are perhaps the subfusoid bodies mentioned in Bourdot and Galzin's first description. I am inclined to interpret them as galls caused by a parasitic fungus. Dr. F. K. Sparrow, to whom the sketches were submitted, suggested that they might possibly represent a *Woronina* parasitic on the *Platyglea*.

Platyglaea fusco-atra Jackson & Martin, sp. nov. (FIG. 6)

Pustulata, gelatinosa, confluens, humescens brunneo-ochracea, sicca fusco-badia; basidiis cylindraceis, $22-25 \times 2.5-3.5 \mu$, transverse 3-septatis; paraphysibus cylindraceis, 2μ cr.; basidiosporis ovatis vel lachrymatis, $5.5-6 \times 4-4.5 \mu$, per repetitionem germinantibus.

Pustulate, the pustules circular, 0.5–1.5 mm. in diameter, then anastomosing in reticulate fashion, soft waxy-gelatinous, yellow-brown when moist, becoming dark reddish brown or blackish and horny when dry; paraphyses cylindrical, $25-30 \times 2 \mu$, each with a prominent clamp connection at base; probasidia cylindrical-clavate, often ventrally swollen, then cylindrical, $22-25 \times 2.5-3.5 \mu$, becoming transversely 3-septate, each cell developing a rather long epibasidium; basidiospores oval or tear-shaped, $5.5-6 \times 4-4.5 \mu$, germinating by repetition.

ONTARIO: Aurora, Oct. 30, 1937, on decayed wood of *Tsuga canadensis*, U. of Tor. 13552. Type.

The dark color, the reticulate pattern and the small basidia accompanied by the coarse paraphyses with the prominent clamp connections should make this species easy of recognition.

Platyglaea pustulata Martin & Cain, sp. nov. (FIG. 7)

Gelatinosa, pustulata, 1–3 mm. diam., humescens alba, sicca cornea, inconspicua; hyphis hyalinis, tenuibus; hypobasidiis cylindratoclavatis, demum transverse uniseptatis; epibasidiis cylindratis, elongatis, 3μ diam.; basidiosporis cylindratis, curvulis, $20-22 \times 5-6 \mu$.

Gelatinous, pustulate, 1–3 mm. in diameter, becoming larger by confluence, pure white varying to dingy white or grayish when soaked, drying to an inconspicuous horny film; in section composed of radiating, branched hyphae, some of the branches becoming slender, branched paraphyses $2-2.5 \mu$ in diameter, others swollen at the tips, the swellings either proliferating or developing into cylindrical-clavate probasidia mostly $30-35 \times 6-7 \mu$, these becoming transversely 1-septate, each cell sending out a cylindrical epibasidium variable in length but usually rather long and $2-3 \mu$ in diameter except just below the sterigma where it is often somewhat enlarged; basidiospores cylindrical-allantoid, often strongly curved, $(16-)20-22 \times (4-)5-6 \mu$.

QUEBEC: Duchesnay, Aug. 24, 1938, on bark of *Abies balsamea*. Type.

ONTARIO: Lake Temagami, Aug. 10, 1939, on coniferous wood, R. F. Cain (U. of Tor. 14977); Algonquin Park, Sept. 9, 1939, on bark of *Abies balsamea*, R. F. Cain (U. of Tor. 14978).

Differing from previously known species of *Platyglea* in the 2-celled basidia and the slender, often strongly curved basidiospores. The empty hyphae below many of the basidia are more or less swollen in such a way as to suggest the empty probasidia of *Jola* (FIG. 7c, center). These are not always present, however, and there may occasionally be two of them. It seems evident that a basidium may start to form when the fructification is beginning to dry and then, when a rain causes the jelly to swell, it proliferates, forming a new basidium near the new surface. Möller (Proto-basidiomyceten, pl. 4, FIG. 5b) shows a similar empty hypha under a basidium of *P. blastomyces*. In the present species the empty walls of the old vesicle frequently surround the proliferation, much as the old walls of an emptied sporangium in *Saprolegnia* surround the new sporangium. In the mounts, numerous basidia are completely detached from their basal hyphae and it seems probable that they may readily be detached in nature when the basidiocarp swells. This is borne out by the way in which some of such detached basidia bear the epibasidia at the basal and distal ends (FIG. 7a). The regular alternation of protoplasm and vacuoles in the paraphyses gives these structures a characteristic and striking appearance, especially under a low power objective.

***Helicobasidium candidum* sp. nov. (FIG. 8)**

Resupinatum, maculiforme dein effusum, tenue, arcte adhaerens, immarginatum, album, subfarinaceum; contexto laxo ex hyphis nodosis, 2-3 μ cr. compositis; basidiis clavatis, saepius curvatis vel varie flexis, quadricellularibus, 60-65 \times 12-13 μ ; sporis ovatis, 18-20 \times 14-15 μ .

Resupinate, pure white, at first floccose, then expanding and anastomosing, finally broadly effused, thin, arid, with indeterminate arachnoid margin, the older portions very faintly yellowish when soaked; in section up to 250 μ thick at center, thinning to a mere subiculum at margins; basidial layer originating under epidermis and erumpent from lenticels, covered by a loosely woven pseudo-tissue of gelatinous hyphae, mostly 2-3 μ in diameter, with clamp connections at many of the septa; surface sterile; basidia at first broadly ovate, then cylindrical, straight or tortuous to strongly

recurved, becoming 4-celled by the formation of transverse septa, $60-65 \times 12-13 \mu$; basidiospores broadly ovate, somewhat flattened ventrally, $18-20 \times 14-15 \mu$. Germination not observed.

QUEBEC: Duchesnay, Aug. 26, 1938, on dead branches of standing *Acer*. Type.

Apparently closest to *H. farinaceum* Höhnelt, but differing in its nearly pure white color, much larger basidia, the somewhat longer and much thicker spores and the numerous clamp connections.

The surface of the fructification is sterile, bearing a very few old, emptied basidia (FIG. 8d), while the numerous young basidia are developing in a basal layer, suggesting that after an early fruiting stage the fungus was preparing for a second fruiting period when collected. Very few spores were seen and none of these were attached, so it is by no means certain that those associated with the fungus really belong to it. On the other hand, the species is so distinctive that it seems justifiable to name it.

The huge, septate basidia suggest the spores of *Delortia*, which Patouillard (Bull. Soc. Myc. Fr. 4: 43. 1888) at first grouped with the Auriculariaceae, later (Tax. Hymen. 33: 1900) removing it to the Hyphomycetes, a decision confirmed by Linder (Ann. Missouri Bot. Gard. 16: 338. 1929). At the base of each basidium is a slender stalk cell, apparently derived from the original probasidium, since the clamp connection is borne at its base (FIG. 8a).

Large clavate or obpyriform bodies are associated with the fructification and at first suggest cystidia. Their occurrence is too irregular, however, to make this seem possible. Some have homogeneous contents (FIG. 8f), others are filled with a tangle of hyphae (FIG. 8g) and still others with rather irregular, globose, spore-like bodies (FIG. 8h). I believe they are galls of a parasitic fungus similar to those observed on *Platyglea Peniophorae* but certainly not the same.

***Ceracea canadensis* Jackson & Martin, sp. nov. (FIG. 9)**

Effusa, ceracea, adnata, tenuis, laevis, ex lutea aurantiaca, ambitu albo floccoso; hyphis $2.5-3.5 \mu$, copiose nodulosus; probasidiis anguste clavatis, $30-33 \times 3.5-4 \mu$; epibasidiis, $20-30 \times 2.5 \mu$; basidiosporis hyalinis, cylindraceis, rectis vel subarcuatis, haud septatis, $11-13.5 \times 4.5-5 \mu$.

Effused in small patches, the largest 30×8 mm., deep chrome (R) in older portions, fading to light orange (R) toward the margin; margin white, floccose; surface pulverulent, cracking, becoming waxy when soaked but not gelatinous; in section $175\text{--}200\ \mu$ thick, consisting of a loosely interwoven basal portion arising directly from the substratum, composed of erect, branching hyphae $2.5\text{--}3.5\ \mu$ in diameter bearing numerous clamp connections, supporting a dense hymenium, $45\text{--}50\ \mu$ thick, mainly of basidia, but including a few cylindrical, paraphysis-like filaments $2\text{--}3\ \mu$ in diameter, arising from the same branches as the basidia; probasidia, at maturity, mostly $30\text{--}33 \times 3.5\text{--}4\ \mu$, giving rise to two rather long epibasidia $20\text{--}30\ \mu$ long and $2.5\ \mu$ in diameter; basidiospores cylindrical, straight or curved, unseptate, with prominent apiculus, $11\text{--}13.5 \times 4.5\text{--}5\ \mu$; germination not observed.

ONTARIO: Port Alexander, Sept. 13, 1939, on coniferous wood (U. of Tor. 14103), Type; Algonquin Park, Sept. 11, 1939, on conifer. R. F. Cain (U. of Tor. 14976).

Brasfield (Lloydia 3: 106–108. 1940.) has concluded that *Ceracea* is a valid genus. The present species seems clearly distinct from any of the few species previously recognized.

STATE UNIVERSITY OF IOWA,
IOWA CITY

EXPLANATION OF FIGURES

Except where otherwise noted, all figures drawn with aid of camera lucida at a magnification of $\times 2400$ and reduced in reproduction to approximately $\times 1000$.

FIG. 1. *Sebacina rimosa*. *a*, probasidium; *b*, septate, thick-walled hypobasidium; *c*, 4-celled basidium; *d*, 2-celled basidium; *e*, 4-celled basidium with segments separating; *f*, basidiospore germinating by repetition; *g*, basidiospore germinating to form mycelium with clamp connections; *h*, two gloeocystidia.

FIG. 2. *Sebacina Pini*. *a*, mature 4-celled basidium with young basidiospore; *b*, probasidium with involucreal sheath presumably formed of gelatinized walls of spent basidia; *c*, tip of paraphysis; *d*, four basidiospores, two germinating by repetition; *e*, two gloeocystidia, the lower one septate.

FIG. 3. *Tremella mycophaga*. *a*, typical detached basidium; *b*, septate, thick-walled hypobasidium, the segments ready to separate; *c*, basidiospore-like body apparently derived from segment of such a basidium as preceding; *d*, three basidiospores; *e*, hypha with clamp connections bearing probasidium and conidia; *f*, seven detached conidia, one germinating by budding; *g*, internal hypha with clamp connection.

FIG. 4. *Tremella simplex*. *a*, typical basidium; *b*, probasidium and small basidium; *c*, fusiform, transversely septate hypobasidium; *d*, hypha bearing both basidia and conidia; *e*, conidia.

FIG. 5. *Platyglea Peniophorae*. *a*, basidium; *b*, young probasidium and crozier-like hyphal tip; *c*, cluster of conidiophores with basidium; *d*, young basidiospore and old, thick-walled basidiospore; *e*, unusually large basidiospore; *f*, swollen hypha with parasitic thallus near tip, and lateral gall with columellate axis; *g*, gall at base of basidium.

FIG. 6. *Platyglea fusco-atra*. *a*, cluster of young basidia; *b*, mature basidium; *c*, three spores, one germinating by repetition; *d*, paraphysis.

FIG. 7. *Platyglea pustulata*. *a*, detached basidium developing epibasidia at either end; *b*, two basidiospores; *c*, three basidia, two detached and three basidiospores. *c*, $\times 460$.

FIG. 8. *Helicobasidium candidum*. *a*, basidium; *b*, clamp connection; *c*, five basidia and clamp connection; *d*, spent basidium; *e*, three basidiospores; *f*, parasite, early homogeneous stage; *g*, same, intermediate stage; *h*, same, late stage. *c* to *h* inclusive, $\times 460$.

FIG. 9. *Ceracea canadensis*. *a*, two basidia and paraphysis; *b*, four basidiospores.

STUDIES IN THE GASTEROMYCETES. I. THE GENUS *DICTYOCEPHALOS*

W. H. LONG AND O. A. PLUNKETT

(WITH 13 FIGURES)

This paper discusses the taxonomic position of *Dictyocephalos*, lists its synonyms, gives an emended description of genus and species, and records new data on its occurrence and distribution.

The family *Tylostomataceae* as defined by Cunningham (1932) contains those genera which have a sporocarp elevated at maturity upon a definite elongated stem, the walls composed of two layers, the exoperidium and the endoperidium, and the gleba consisting of spores and a well developed capillitium (with one exception). Six genera were placed by Cunningham in this family as follows: *Battarrea*, *Chlamydo pus*, *Phellorina*, *Podaxon*, *Queletia* and *Tylostoma*. The genera *Dictyocephalos* and *Schizostoma* should be added since they have all the characters assigned to this family. The following synopsis shows the relationship existing between *Dictyocephalos* and the other genera in the family.

KEY TO THE FAMILY TYLOSTOMATACEAE

(adapted from Cunningham)

1. Basidia in fasciculate clusters, persistent at maturity 2
1. Basidia not fasciculate, disappearing at maturity 3
2. Sporocarp traversed by an axile columella *Podaxon*.
2. Sporocarp carried at apex of stem, columella none 4
4. Exoperidium continuous with stem, endoperidium a cupulate extension of the stem apex *Phellorina*.
4. Exoperidium not continuous with the stem, sporocarp seated on the truncate expanded stem apex, stem volvate 5
5. Gleba not cellular, dehiscence by an apical stoma *Chlamydo pus*.
5. Gleba cellular, dehiscence by the irregular breaking away of the peridium *Dictyocephalos*.
3. Elaters present in the gleba *Battarrea*.
3. Elaters not present in the gleba 6
6. Sporocarp with a definite apical stoma *Tylostoma*.
6. Sporocarp dehiscing irregularly *Queletia*.
6. Sporocarp dehiscing by irregular stellate rays *Schizostoma*.

The genus *Dictyocephalos* was erected by Underwood (1901) on specimens collected by E. Bethel in Colorado in 1897.

Dictyocephalos Underwood, Bull. Torrey Club 28: 441. 1901.

Battareopsis P. Henn. Hedwigia Beibl. 41: 212. 1902.

Whetstonia Lloyd, Myc. Writ. 2: 259. 1906.

Sporophore hypogeous, enclosed in a volva during early stages of growth, erumpent as maturity approaches; *stipitate*, stem stout, solid, becoming woody; *peridium* of two layers, outer (exoperidium) roughened, inner (endoperidium) coriaceous to membranaceous, seated on the expanded discoid apex of the stipe; *dehiscence* by the irregular breaking away of the peridium; *gleba* powdery, having permanent cells, spores, and persistent fascicles of basidia, true capillitium none; *spores* globose to subglobose, fulvous, verrucose.

HABITAT: Growing solitary or in groups of 2-5 individuals, in sandy or adobe alkaline soil, in arid or semi-arid regions.

TYPE SPECIES: *Battarreia attenuata* Peck.

DISTRIBUTION: North America; Africa.

***Dictyocephalos attenuatus* (Peck) comb. nov.**

Battarreia attenuata Peck, Bull. Torrey Club 22: 208. 1895.

Dictyocephalos curvatus Underwood, Bull. Torrey Club 28: 441. 1901.

Battarcopsis Artini P. Henn. Hedwigia Beibl. 41: 212. 1902.

Whetstonia strobiliformis Lloyd, Myc. Writ. 2: 259. 1906.

Phellorina strobilina as shown by Lloyd, Myc. Writ. 5: 735. 1917.

Sporophore 7 to 56 cm. tall, originating 4 to 20 cm. below the surface of the soil, often with 1-2 white cord-like roots; *sporocarp* globose to subglobose, depressed, often irregular, 2-6 cm. high by 5-13 cm. broad, seated on the discoid apex of the stipe, basal portion hard, thick, with the narrow margin usually concave beneath; *the discoid apex*, when freed of gleba light tan to white, convex and coarsely reticulate by the boundary walls of broad shallow pits (FIG. 1); *exoperidium* fleshy to gelatinous when young, developing horny to subcartilagenous scales with age which may be small and more or less persistent (FIGS. 4, 9), or large 4-5 sided pyramidal warts (FIG. 2) 1-2 cm. broad by 1-1.5 cm. tall, normally deciduous,

leaving a decided scar on the endoperidium (FIG. 6); *endoperidium* 1–2 mm. thick, basal portion often coriaceous and persistent, upper part membranous, brittle when dessicated, dehiscing by breaking into irregular pieces which soon fall away leaving the gleba exposed (FIGS. 3, 10); *stipe* curved, sometimes straight, 5–52 cm. tall,

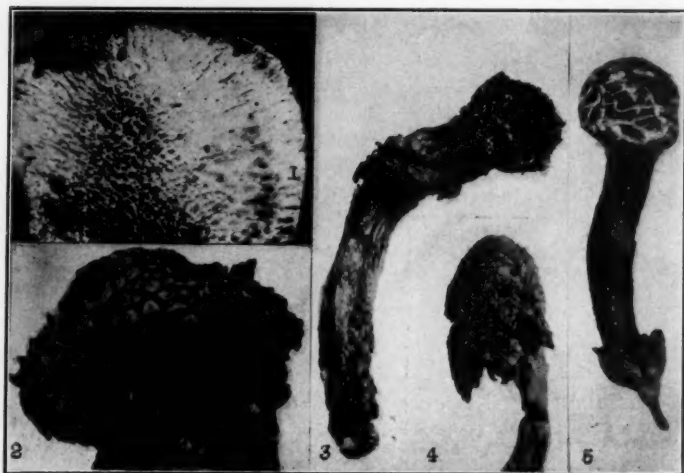


FIG. 1. The white reticulate-pitted upper surface of the discoid apex of stem. California plant, 1936 crop, $\times 9/10$. 2, large pyramidal warts of exoperidium. California plant, 1938 crop, $\times 5/8$. 3, sporophore with naked cellular gleba and coarse annulus, New Mexico plant, $\times 2/5$. 4, coarse veil and the small scales of the exoperidium, New Mexico plant, $\times 3/7$. 5, plant with radicating base, cupulate volva and brown flakes of exoperidium on the whitish endoperidium, California plant, 1939 crop, $\times 3/8$.

2–5 cm. thick at top, 1–4 cm. at bottom, solid (except where hollowed out by insects), terete, or flattened, often deeply sulcate, usually attenuate below, subfleshy, drying subcoriaceous to woody, context when young, white becoming walnut brown to vandyke brown with age,¹ outer surface uneven and peeling, often with coarse, spreading or reflexed scales (FIGS. 6, 8) caused by the outer layers of the stipe cracking both transversely and longitudinally from weathering, base of stipe often pointed and becoming entirely free from the enclosing volva (FIG. 7); *volva* persistent, usually cupulate (FIG. 5) to obconic, sometimes tubular, laciniate-incised, 3–11 cm. tall by 4–8 cm. wide at top, walls 2–4 mm. thick,

¹ Ridgway, R. Color standards and color nomenclature, p. 1–111 plus 1–43, 1912.

rupturing from 2-8 cm. below surface of soil, thereby exposing the ascending sporocarp to the dirt for this distance during elongation, walls apparently composed of three layers, inner layer a thin tissue which deliquesces into a blackish fluid just preceding and during elongation, median layer semigelatinous when young, becoming horny with age, outer layer white to tan, hard, chalky in texture; *gleba* foetid, with odor of decaying fish, pecan brown to mikado brown (after Ridgway), cellular (FIG. 10), cell wall white, fragile, membranous, composed of a hyaline amorphous central tissue overlaid by a dense network of branching colorless to fulvous hyphae, easily fragmenting and falling away in lacinate irregular flakes and shreds, cell walls in bottom of the gleba thicker, firmer and more permanent, often persisting as broad, flattened, pointed teeth on the exposed convex surface of the glebal floor long after the gleba has disappeared; *capillitium*, free capillitium absent, but the hyphae composing the outer layers of the glebal cell walls may break loose and simulate capillitial threads; *spores* globose to subglobose, 5-7 microns, walls thin, fulvous, verrucose; *basidia* clustered bearing 1-4 spores on short sterigmata.

TYPE LOCALITY: Nevada, United States of America.

DISTRIBUTION AND SPECIMENS

AFRICA:

EGYPT. Alexandria, in Villa des Tito: *Artin-Pascha-Jacob*, Dec. 1901. 1 specimen in Berlin Mus., Type of *Battareopsis Artini* P. Henn.

SOUTHWESTERN MOROCCO. Goulimine, 1936. 1 specimen in Herb. Lab. Crypt. Mus. Nat. d'Hist. Nat. Paris, France, under name *Dictyocephalos curvatus*.

SOUTHERN RHODESIA. Wankie District (county), Wankie, elev. 2448 ft., *Albert Giese*, 1916, comm. *Miss A. V. Duthie*. 1 specimen ($\frac{1}{2}$ plant) in Lloyd Myc. Coll., Washington, D. C., under name *Phellorina strobilina*. The other half of this plant is in the Nat. Mus. of Southern Rhodesia at Bulawayo.

NORTH AMERICA:

NEVADA. C. W. Irish, comm. Dr. Thomas Taylor, 1895. 1 specimen in New York State Mus., Albany, Type of *Battarreca attenuata* Peck.

COLORADO. Grand Co. Colorow, 4 miles south of Kremmling, elev. 7800 ft., E. Bethel, August, 1897; several plants (at

least 3) in New York Bot. Garden, Type of *Dictyocephalos curvatus* Underwood; 3 plants (fragments) in Myc. Coll. Bureau Plant Industry, Washington, D. C., Reliquiae Betheli-anae, Ex type collection of *D. curvatus*; 1 plant in Lloyd Myc. Coll. (5634), E. Bethel, 1897, part of type collection; a pinch of gleba and a prepared microscopic mount in Lloyd Myc. Coll. (98829), taken by Lloyd from Type at New York Bot. Garden. All under name of *D. curvatus*.

MINNESOTA (?). Comm. Dr. Mary S. Whetstone, 1906. 1 specimen ($\frac{1}{2}$ plant) in Lloyd Myc. Coll., Type of *Whetstonia strobiliformis* Lloyd. The other half of this type specimen is in the Patouillard Herb. at the Farlow Herb. (1324).

NEW MEXICO. Sandoval Co., 5 miles west of San Ysidro, on State Highway 44, elev. 6200 ft., W. H. Long, Oct. 25 and Nov. 1, 1927. 3 plants in Long Herb. (8053 & 8054).

CALIFORNIA. Los Angeles Co., 5 miles east and $2\frac{1}{2}$ miles north of Lancaster, elev. 2350 ft., O. A. Plunkett & W. H. Long, June 1, 1938; 75 plants in Long Herb. (8230); O. A. Plunkett, Sept. 9, 1938; 17 plants in Long Herb. (8231) and Oct. 5, 1938; 50 plants, of which 18 are in Long Herb. (8344), 28 in Plunkett Herb. at Los Angeles, and 4 plants in Herb. of Herbert Granquist, Lancaster, Calif., W. H. Long, August 24-27, 1939; 987 plants of which 985 are in Long Herb. (8436 & 8437) and 2 plants in Herb. of Paul & Marion Rea (210), Santa Barbara, California. The above distribution of *Dictyocephalos* shows a range in altitude from near sea level at Alexandria, Egypt, to 7800 feet in Colorado.

THE SYNONYMY OF *DICTYOCEPHALOS ATTENUATUS*

Battarreia attenuata Peck. The original description of this species agrees in every particular with our plant even to the number of individuals found in the tufts and also in the strong foetid odor of the gleba. Peck's description was made from a single old dried plant and from notes furnished by the collector. The type specimen should be in the New York State Museum but it has been misplaced.

This plant does not belong to the genus *Battarreia*, as now de-

fined, but does agree in all essential characters with *Dictyocephalos*. It is therefore transferred to this genus as *Dictyocephalos attenuatus*.

Dictyocephalos curvatus Underwood. An examination of a part of the type collection shows that our plants are identical with it. The species name, *D. curvatus*, can not be retained since it is antedated six years by Peck's *Battarreia attenuata*.

Battareopsis Artini P. Henn. The writers have not examined this material but the original description, and the illustrations of the plant by Lloyd (1898-1925), agree fully with *Dictyocephalos attenuatus*; it has the cellular gleba, the reticulate discoid apex of the stipe, woody stem, horny volva, persistent fascicles of basidia and the same type of spores. Nothing is known of the peridium or method of dehiscence, since these characters were destroyed when the plant emerged.

Whetstonia strobiliformis Lloyd. The senior author examined the type in the Lloyd Myc. Coll. and found that it had all the characters of *D. attenuata* even to the peculiar structure of the walls of the glebal cells. The specimen is unusual in having a stipe with a bulbous base; three of the California plants have bulbous bases similar to the Minnesota specimen.

Phellorina strobilina in part: while studying the specimens listed as *Phellorina* in the Lloyd Myc. Coll., the senior writer found one plant which did not belong to this genus. It had the following legend; "Cat. No. 30315 Lloyd Collection, *Phellorina strobilina*, Stellenbosch, S. Africa, Coll. Miss A. V. Duthie, det. C. G. Lloyd." The specimen has the typical cellular gleba, same structure of the glebal cell walls and all other characters of *Dictyocephalos attenuatus*. The sporocarp is 6 cm. broad by 4 cm. high, covered with pyramidal warts, and is seated on the expanded discoid apex of the stipe. The plant does not have the urceolate extension of the apex of the stem nor the exoperidium continuous with the exterior of the stipe as is the case in the genus *Phellorina*. This is the plant that Lloyd shows in his Myc. Writ. 5: 735, f. 1101 under name *Phellorina strobilina*.

The photograph of the type of *Phellorina strobilina* (Kalch.) as shown by Lloyd in his Myc. Writ. 1: pl. 27, f. 3 is very similar in general appearance to *Dictyocephalos attenuatus* and might well

be this plant if the gleba were cellular, in which case the species name of our plant would have to be changed to *Dictyocephalos strobilinus* (Kalch.).

DISCUSSION AND HISTORY OF THE VARIOUS COLLECTIONS

The Egyptian plant, *Battarcopsis Artini*, was collected at Alexandria, Egypt, growing under an asphalt pavement 2 cm. thick, on

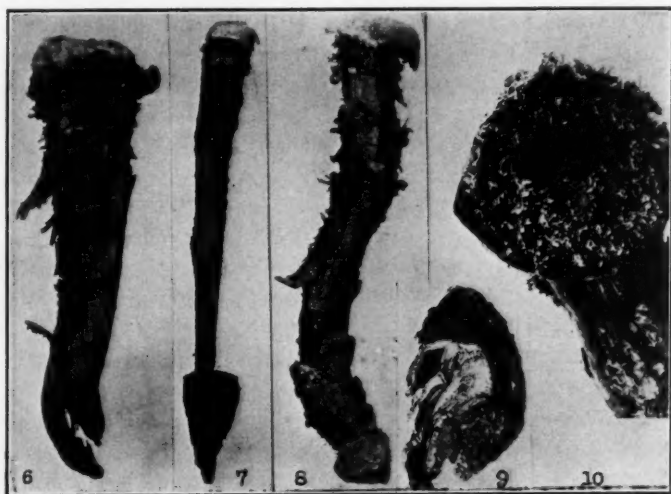


FIG. 6. Scars on endoperidium where the warts of exoperidium peeled off, also shows the rough scales on stipe. California plant, 1937 crop, $\times 1/3$. 7, a slender very attenuate plant with a pointed stipe free from the obconic volva. California plant, 1935 crop, $\times 1/3$. 8, a curved sporophore with a scaly stipe and knob at base where volva was attached. California plant, 1937 crop, $\times 1/3$. 9, longisecton view showing the overhanging margin of the pileus and the small scales of the exoperidium. New Mexico plant (reverse side of figure 4), $\times 3/7$. 10, gleba showing the permanent cells with membranous walls. New Mexico plant, $\times 1$.

emerging it cracked the asphalt for a radius of 50 cm. around the plant. This specimen apparently reached Berlin in 3 separate pieces, the volva, stem and cap as shown by Lloyd, Myc. Writ. 1: pl. 22. The volva on this plate (FIG. 2) is tubular and not flaring as illustrated by Hennings (1902) in Hedwigia page 213; also the stipe in this drawing is apparently reversed as to position,

the small end should be inside the volva and the large end attached to the cap, since the plant was probably attenuate toward the base, as is usual in this species.

The Moroccan plant, *Dictyocephalos curvatus*, as figured and discussed by Malençon (1935-1936), was discovered by a native collector in the environs of Goulimine in the southwestern part of French Morocco, to the north of the province of Rio de Oro. Only one plant, an old deformed one, was found growing in alkaline soil in a hot semi-desert region. The stipe was bent near the top with the sporocarp split into three distinct heads or lobes, each lobe bearing some gleba. Similar plants with 2- to 4-lobed sporocarps are present in the California collections. This Moroccan plant is undoubtedly *Dictyocephalos attenuatus*.

The Rhodesian specimen, called by Lloyd *Phellorina strobilina*. Dr. G. Arnold, Director of the National Museum of Southern Rhodesia at Bulawayo, says in a recent letter that this specimen was collected on a road near or in Wankie which is situated on the line from Bulawayo to Victoria Falls about Lat. 18° S. and Long. 27° E. in the geological formation known as the Karroo System.

The Nevada material, *Battarrea attenuata* Peck, was found commonly growing in tufts of 3 to 5 individuals in dry sandy soil. The plants were almost wholly buried in the ground, appearing above the surface only in seasons after heavy snow-falls had melted gradually and moistened the earth deeply. The locality in Nevada where the plants were found is not recorded.

The Colorado plants were found by Bethel in an arid region in the northwestern part of Colorado growing in soft, alkaline adobe soil, destitute of any other vegetation. Some plants were entirely out of the ground while others were standing about one inch deep in the soil. Some had stems much bent, others were twisted like a corkscrew with portions of the stalk split and bent back. Bethel found fragmentary remains of this species quite abundantly in many places on arid mesas of western Colorado near the Utah line.

The Minnesota specimen, *Whetstonia strobiliformis* Lloyd. Only one plant was found and it probably was not collected in Minnesota, but from some place farther south in an arid or semi-arid country since all other known collections have been found in

such regions. The senior writer tried to learn the actual source of the Minnesota plant but without success.

The cavities in the stem of this specimen were caused by insects as evidenced by the dark brown frass still present. The overhanging margin at the base of the exoperidium is very similar to

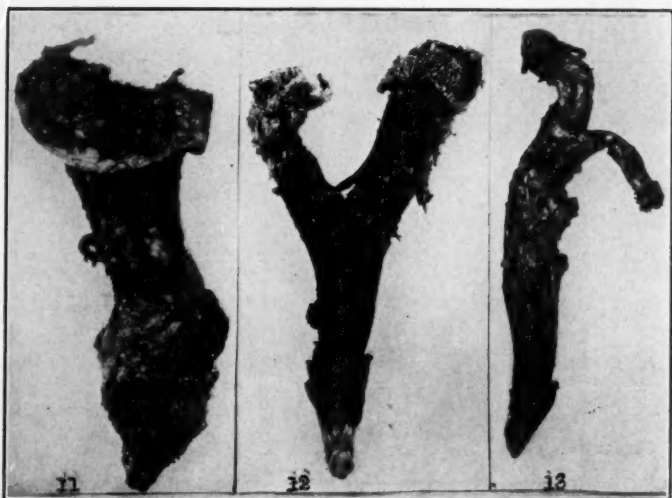


FIG. 11. A sporophore destitute of a true volva, only a mass of dirt held together by mycelial hyphae at base of stipe. California plant, 1938 crop, $\times 1/2$. 12, a forked plant with radicating base and obconic volva. California plant, 1936 crop, $\times 1/4$. 13, a large plant with one side branch and the stub of a second branch below the first one. California plant, 1938 crop, $\times 1/3$.

that on one of the New Mexico plants (FIGS. 4, 9). Lloyd gives some good illustrations of this plant in *Myc. Writ.* 2: *pl.* 90, *f.* 1-5. The specimen in the Lloyd *Myc. Coll.* does not have a volva and the base of the stipe indicates that if one were present when young it was not very pronounced. Two similar plants, without any signs of volvas (FIG. 11), were found in the California material, although companions in the same collections have well developed volvas.

The New Mexico specimens. The three plants of this collection were fresh, having just emerged when found. They were grow-

ing in an open unshaded area at the lower end of a long shallow wash in the alkaline soil deposited by the water, 100 yards outside of the eastern boundary of the Ojo del Espiritu Santo Grant on state Highway 44.

The plants differ considerably as the following data show. The larger one has an irregular, thin, brittle, erect collar around the base of the exposed gleba; a rough lacerate annulus 2-4 cm. below the sporocarp, consisting of pieces of the peridium and the outer layers of the stem which tore loose during elongation (FIG. 3); the scales of the exoperidium are large coarse warts 10-15 mm. wide by 3-5 mm. high. The second plant does not have either a collar or an annulus, but has a wide overhanging margin at base of pileus with remnants of the torn walls of the stipe and of the peridium forming a coarse veil (FIG. 4); scales of exoperidium thin, small, 3-5 mm. across. The third plant is stout, deformed and split lengthwise just below the sporocarp with the outer layers of stem stripped off and carried up on the lower margin of the pileus as an imperfect veil. The glebas of all three plants have the foul odor of decaying fish which still persists in the dried specimens after 12 years in the herbarium. The exoperidium was apparently viscid during elongation, since particles of dirt are still firmly attached to portions of its surface.

The area where these plants were collected has been scouted every year since then, but no others have been found.

The California collections. The California area was discovered by the junior author in December 1937 while rabbit hunting but no specimens were taken. In June 1938 both authors visited the area and gathered material, later other trips were made until five collections of *Dictyocephalos attenuatus*, comprising 1129 plants, were obtained. All were growing in a friable soil, ashy in color and texture, on or adjacent to, slightly elevated areas which appear as islands or ridges of land, underlaid by an alkaline clay hard pan. Many plants were in the partial shade of *Atriplex* bushes but the majority were in open naked areas between the *Atriplex* plants.

Four collections were made in and along the sides of a broad shallow wash, over an area of about ten acres; while collection no. 8436, consisting of 80 plants, was found scattered over some 40

acres about $\frac{1}{2}$ mile southwest of the other area in the same type of soil and environment.

Three very unusual specimens were found on the California area; one is a plant with a forked stem (FIG. 12), another is a large thick plant with two small side branches (FIG. 13), while the third specimen has a volva bearing twin plants each perfect in every way.

The California collections have many plants with scales of the exoperidium small and flat, others have flat to erect scales while a few have large erect pyramidal warts (FIG. 2). The outer peridium (not the volva) apparently is fleshy to semigelatinous just before emergence and often very thick on top. As the plant matures and elongates this fleshy layer cracks into scales or warts of varying sizes which are often flattened or otherwise deformed when pushing through the soil, or they may have hardened sufficiently to emerge uninjured. Many exoperidia are horny, reddish and semi-translucent, especially if they were subjected to much pressure when elongating. The degree of this pressure would vary with the hardness of the soil and the depth below the surface at which the plants originated. Exoperidia damaged during emergence usually remain attached to the inner peridium, falling with it when dehiscence occurs.

Many weathered specimens were found, some probably 25 to 30 years old. Only two fungi were observed on these plants, a brownish black mould and a red species of *Gymnoascus*(?) on the old volvas, neither of these fungi caused any evident disintegration of the *Dictyocephalos* tissue. Apparently the main agents in the destruction of the old plants are insects and the action of the elements. Termite work is evident on many and a species of carpenter ant (*Camponotus*) was found in some, but the principal agency in the disintegration of the plants is the weathering action of wind, rain and other climatic factors. The destruction of the plants, however, is a very slow process requiring years before they are finally reduced to soil.

GENERAL REMARKS

Data compiled from the various collections show wide variations in this unique species; the three largest plants are 47 cm., 50 cm.

and 56 cm. tall, the three smallest ones 7 cm., 9 cm., and 13 cm., while the usual sizes range from 20–30 cm. in height; 732 stipes are terete, 450 flattened, 241 sulcate; 514 attenuate below, 29 taper upward, 207 are uniform in size throughout, 3 are bulbous at base; 661 are solid while 407 have cavities produced by insects. The heads (expanded apices of the stipes) have narrow margins, ranging from 3 to 30 mm. wide, the usual size being 8–10 mm. In some plants portions of the margin curve upward for 2–3 cm. like the remnants of a shallow cup (FIGS. 6, 12) but never around the entire rim of the head. The tops of the heads vary as follows, 628 are convex, 47 concave, 91 wedge-shaped, 92 dome-like, 17 flat, and 24 spoon-shaped; in outline, 31 heads are oblong, 32 reniform, 15 arrow-shaped, 7 triangular, the balance are orbicular to oval. Eleven plants have sporocarps split into 2–4 finger-like lobes, each lobe having its own gleba; 1 plant has an annulus (FIG. 3), 2 have veils (FIG. 4), 7 have forked stems (FIG. 12), 6 plants have 1–2 side branches (FIG. 13) while 6 have volvas bearing twin plants.

The scales of the exoperidia vary greatly, ranging from small, thin ones 3–5 mm. across by 0.5 mm. thick (FIGS. 4, 9), as in two of the New Mexico plants, to large pyramidal warts 1–2 cm. broad by 1.5 cm. tall seen in numerous California specimens (FIG. 2) and in the Rhodesian plant. Many have scales intermediate between these two extremes while some have large warts above with small scales around the lower part of the same sporocarp.

The amazing variations in size, shape, scales and other characters of these plants are so many that numerous "new" species could be made from aberrant individuals by writers who believe such characters are valid criteria for differentiating species.

The foetid odor of the gleba so characteristic of this species is present in all the California plants, even in those which had been covered with water for 12 hours during the 1938 floods (March 2–3). Another outstanding character of this species is the tan to white (when weathered) coarsely reticulate-pitted upper surface of the discoid apex or head of the stipe (FIG. 1). This whitish surface consists of a thin (0.1 mm. thick) membrane beneath which is the usual brown color of the stipe context. This thin membrane also lines the entire inside of the endoperidium.

The majority of the plants collected in June 1938 were in open unshaded areas where groups of 2-4 individuals were found emerging from the same hole in the ground which was made by the plants as they elongated; some of the raised blocks of soil weighed 15 pounds. These groups apparently originated from a common underground mycelium, each plant being a complete individual as to volva, stem and sporocarp. The plants of the 1939 crop were not in groups but were solitary and often in more or less shaded places under the edges of the *Atriplex* bushes.

The California specimens grew in Antelope Valley on the edge of the Mojave Desert—a very hot and arid region—where temperatures during June, July and August range as high as 110 to 115 degrees F. The rainfall for the past ten years has varied from three to twelve inches, the average being near seven inches per year.

ACKNOWLEDGMENTS

The writers wish to make grateful acknowledgments to Mr. John A. Stevenson for loan of material, negatives and helpful suggestions on the Bibliography; to Dr. G. D. Darker for aid on the Bibliography; to Mr. and Mrs. Herbert Granquist for aid in collecting specimens; to Floyd R. Schroeder for making the photographs for figures 3, 4, 9, 10; and to W. Carter Maxwell and Glenn R. Haynes of the Division of Grazing for assistance in making the photographs for all the other figures in this article.

ALBUQUERQUE, NEW MEXICO,

AND

DEPARTMENT OF BOTANY,
UNIVERSITY OF CALIFORNIA
AT LOS ANGELES

BIBLIOGRAPHY

- Clements, F. E. The genera of fungi, 227 p. Minneapolis. 1909.
Clements, F. E. & Shear, C. L. The genera of fungi, 496 p. 58 pl. New York. 1931.
Coker, W. C. & Couch, J. N. The Gasteromycetes of the Eastern United States and Canada, 201 p., 123 pl. Chapel Hill. 1928.
Cunningham, G. H. The family Tulostomataceae. The Gasteromycetes of Australasia no. 14. Proc. Linn. Soc. New So. Wales 57: pt. 1-2: 27-39, pl. 1. 1932.

- Fischer, Ed. Plectobasidiineae (Sclerodermineae), E. & P. Nat. Pfl. 1: 1**, 18 p., 12 fig. 1899.
- . Gastromyceteae. E. & P. Nat. Pfl. II. 7A: 122 p., 91 fig. 1933.
- Hennings, Paul. *Battareopsis Artini* n. gen., sowie andere von Professor Dr. G. Schweinfurth in Aegypten 1901-1902 gesammelte Pilze. Hedwigia Beibl. 41: (210)-(215), 2 fig. 1902.
- Höhnelt, F. von. Resultate der Revision von Paul Henning's Pilzegattungen. Ann. Myc. 9: 166-175. 1911.
- Hollós, L. Gasteromycetes Hungariae. Die Gasteromyceten Ungarn, 278 p., 31 pl. mostly colored, Leipzig. 1914.
- House, E. D. Index to handbooks of Dr. Charles Horton Peck 30 (typewritten). Notebook 18, p. 137. 1923.
- Lloyd, C. G. Mycological writings 1-7. 1898-1925.
- Malençon, G. Etudes sur les phellorines. 1-11. Ann. Crypt. Exot. 8: 1-48, 101-132, pl. 1-6, f. 1-6. 1935-1936.
- Melchers, L. E. A check list of plant diseases and fungi occurring in Egypt. Trans. Kans. Acad. Sci. 34: 41-106. 1931.
- Peck, C. H. New species of fungi. Bull. Torrey Club 22: 198-211. 1895.
- Roumeguere, C. Bibliographie (Review of White, V. S. The Tylostomaceae of North America). Rev. Myc. 25: 90-92. 1903.
- Saccardo, P. A. Elenchus fungorum novorum qui post editum Vol. II, "Sylloge fungorum" usque ad finem Decembris MDCCCXCV innouerunt concessit P. A. Saccardo. Hedwigia Beibl. 35. Report 7: 1-L. 1896.
- Saccardo, P. A. Sylloge fungorum 1-25. 1882-1931.
- Shear, C. L. Our puffballs. III. Asa Gray Bull. 8: 49-53, f. 1-11. 1900.
- Stevenson, J. A. General index to the mycological writings of C. G. Lloyd. Bull. Lloyd Lib. 32, VII. 64 p. 1933.
- Stevenson, J. A. & Cash, E. K. The new fungus names proposed by C. G. Lloyd. Bull. Lloyd Lib. 35 (Myc. Ser.), 209 p. 1935.
- Underwood, L. M. Moulds, mildews and mushrooms, 227 p., col. frontispiece, 9 pl. New York. 1899.
- . See also White, V. S. 1901.
- White, V. S. The Tylostomaceae of North America. Bull. Torrey Club 28: 421-444, pl. 31-40. 1901.

SEXUALITY IN *ACHLYA* AMBISEXUALIS

JOHN R. RAPER¹

(WITH 4 FIGURES)

INTRODUCTION

Experimental proof of heterothallism in *Dictyuchus*, a genus of the Saprolegniaceae, was given by J. N. Couch (1926) more than twenty years after the discovery of heterothallism in the Mucorales by Blakeslee (1904). Since the publication of Couch's work a similar sexual condition has been demonstrated in two additional genera of the Saprolegniales, *Achlya* and *Sapromyces*. Coker (1927) described *Achlya bisexualis* from the unpublished work of A. B. Couch, and this experimental work was duplicated and confirmed with new isolates by the writer (1936).

Heterothallism was demonstrated in *Sapromyces Reinschii* by Philip H. Jordan, of Harvard University, during 1927 to 1929. An account of his work has recently been published as a preliminary note by Weston (1938). For a number of years Bishop (1937) has continued and extended the investigation on the sexuality in *Sapromyces*.

More recently two new "heterothallic" species of *Achlya* have been described, *A. regularis* Coker and Leitner (1938) and *A. ambisexualis* Raper (1939).

Heterothallism in the Mucorales as defined by Blakeslee (1904) and subsequently analyzed by Burgeff (1912) connotes the presence of a single sex in the mycelium and requires the bringing together of two mycelia bearing complementary sexual potentialities before sexual reproduction can be accomplished. In the

¹ Contributions from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 175.

The writer wishes to acknowledge his indebtedness to Professor Wm. H. Weston, Jr., under whose direction the present study was pursued, for his valuable suggestions and criticism.

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germination of the resulting zygote, which has a large number of fusion nuclei, complete segregation of sex takes place insofar as the individual nuclei are concerned, but each spore in the germ sporangium contains several nuclei and hence may have nuclei bearing both plus and minus potentialities. Such a spore, upon germination, gives rise to a thallus of mixed sexual character, known as a heterokaryotic mycelium, with complete segregation taking place in spores subsequently produced.

The sexual condition in the various water molds that have been termed heterothallic does not agree in all respects with conditions first demonstrated in the Mucorales by Blakeslee. An appreciation of the discrepancies existing between allegedly comparable sexual conditions in the two groups necessitates a review of previous work on the water molds.

Couch (1926) found, in *Dictyuchus monosporus*, strains which were ♀, ♂, parthenogenetic, homothallic, and neuter, all having identical morphological characters. As had been repeatedly noted in the Mucorales, Couch found that the ♂ and ♀ plants differed widely in their sexual potency. Further, he found that zygotes produced by matings between a ♂ and a compatible ♀, gave rise to progeny of four different types. The four types found included (1) ♂, (2) ♀, (3) thalli of mixed sexual potentialities which, however, were predominantly ♂ or ♀, and finally (4) sexually inactive mycelia. Oöspores of the parthenogenetic strain gave rise to plants like the parent, which oddly enough, in some few crosses with ♀ mycelia, gave a weak ♂ reaction with the formation of antheridial branches.

Coker (1927) reported that *A. bisexualis* has ♂ and ♀ strains. Raper (1936) showed that in addition to ♂ and ♀ strains two other strains were involved. Plants were isolated which gave a ♀ reaction when mated with a compatible ♂, but which in single spore culture frequently produced abortive oögonia and antheridia. Usually only a few oöospheres were formed in each oögonium and as a rule no oöspores reached maturity. This group of plants was designated hermaphroditic-female. A number of isolates were collected, which were apparently sexually sterile. Since the publication of this account, the author has found two other sexual strains which will be described in detail at a future date.

In *Sapromyces Reinschii*, the heterothallic condition found by Jordan was again not strictly heterothallism as defined by Blakeslee. Both ♂ and ♀ plants were found which reacted sexually when grown together. A number of isolates, however, showed a more complicated sexual condition than a simple bisexual apposition. One isolate produced oögonial initials when grown alone, yet it reacted as a normal ♀ when crossed with a plant known to be ♂. Plants which were apparently neuter were isolated by Jordan. Bishop, later working on the same species, found the males to be sexually stable, but certain of the females used in his investigation produced a few oögonia and antheridia in single culture. Fertilization and the maturation of oöspores sometimes occurred. He suggested that these plants were hermaphroditic-females. Sterile strains were also found, but it was shown that many of the plants thought to be neuter were capable of giving normal sexual reactions when mated with test plants of strong known sexual characters.

A new species of *Achlya*, *A. regularis*, has recently been described as heterothallic by Coker and Leitner (1938). Certain plants of this species, while having definite heterothallic characteristics, at times produced a small number of sexual organs in single culture.

The problem of sexuality in *Achlya* was undertaken by the author at the suggestion of Professors Coker and Couch of the University of North Carolina in 1934, and has been continued since that time in their laboratory and later at Harvard University under the direction of Professor Wm. H. Weston, Jr.

The present paper presents the results of an investigation on the sexuality of *A. ambisexualis* and attempts to interpret and evaluate the sexuality of a number of other water molds previously described as heterothallic.

MATERIALS AND METHODS

The material of *Achlya ambisexualis* used in this investigation comprises the ten isolates from which the description of the species was originally drawn (1939). The isolates were separated on morphological characters into three varieties: type, var. *abjointa*, and var. *gracilis* but since varietal differences have not been cor-

related with sexual behavior, designation of the isolates has been based on sexual rather than morphological characters. The origin, collector, date of collection, and variety of each of the isolates are given in Table I.

TABLE I

Isolate	Variety	Place of Collection	Date of Collection	Collector
1	abjointa	Barton Mills, Eng.	Oct. 1937	R. Emerson
3	abjointa	Chapel Hill, N. C.	Nov. 1935	J. R. Raper
2	gracilis	Blue Hills, Mass.	Oct. 1938	F. T. Wolf
4	type	Charles River, Cambridge, Mass.	Oct. 1937	S. B. Salvin
5	type	Charles River, Cambridge, Mass.	Oct. 1937	S. B. Salvin
9	type	Charles River, Cambridge, Mass.	Oct. 1937	S. B. Salvin
10	type	Charles River, Cambridge, Mass.	Oct. 1937	S. B. Salvin
6	type	Oöspore of No. 5 \times No. 10	Apr. 1938	J. R. Raper
7	type	Oöspore of No. 5 \times No. 10	Apr. 1938	J. R. Raper
8	type	Oöspore of No. 5 \times No. 10	Apr. 1938	J. R. Raper

The methods used in this study are identical with those previously employed (1936) except for a few modifications. These involved: (1) the use of a known salt solution instead of distilled water treated with animal charcoal, (2) the use of a suitable agar medium for matings in addition to the usual matings in water, and (3) a technique of determining the sexuality of new isolates by a simultaneous mating with known ♂ and ♀ strains of two species. The importance of these innovations warrants a brief discussion.

Because of the extreme sensitivity of water molds to the dissolved content of the water in which they grow standardization of the medium used in their culture was necessary. A number of water molds, including *Thraustotheca clavata* and several species of *Achlya*, were grown on hemp seed in the various types of water previously employed by other workers. Vigorous growth of the fungi, however, could not be maintained with predictable certainty in any of the various types. Further tests showed that the desired results could be obtained by using Pyrex glass distilled water to which was added a number of inorganic salts in the following concentrations:

Salt	Molarity	Approximate Percentage
KH_2PO_4	3×10^{-4}	0.00045
MgSO_4	1.2×10^{-4}	0.0003
CaCl_2	10^{-6}	0.0001
FeCl_3	10^{-6}	0.000016
$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	10^{-7}	0.000003

The importance of the use of a standardized "water" in experimentation with water molds cannot be over-emphasized, since variations in the kind and amount of dissolved substances present often bring about definite variations in both vegetative and sexual structures.

To verify the results obtained by mating compatible strains in water the same combinations have been made on a favorable nutrient agar medium. Of a large number of media tried, the one found to be the most suitable was the following:

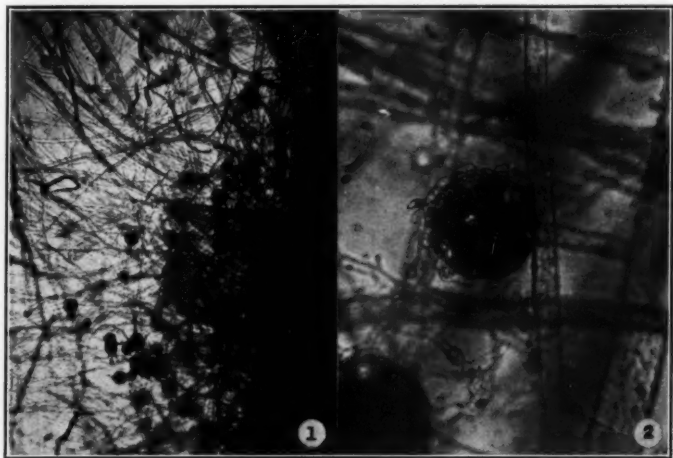
Starch (Soluble).....	3 gms.
Peptone (Difco).....	1 gm.
Hot water extract of 10 gms. of lentils	
Agar (Difco-Bacto).....	20 gms.
Water (containing salts as described above) to.....	1000 cc.

The use of this agar medium for matings eliminates the most serious objection to matings in water. When the plants are mated in water, zoösporangia are produced in abundance and the liberated zoöspores frequently come to rest on the substrate of the opposed strain and there germinate to form a mycelium which, though small, may produce a few sexual organs. This renders accurate determination of the sexual relationships difficult and can only be obviated by repeating the mating until the same unfortunate event does not occur again. In agar matings only a very few zoösporangia are produced, from which the zoöspores never escape. The region of sexual organs is also better defined and more narrow than in water matings.

Another important advantage of this agar medium is that it greatly facilitates carrying on continued matings free of bacterial contamination.

The sexual potentialities of new isolates were determined in the following manner. Previously determined ♂ and ♀ strains of both *A. bisexualis* and *A. ambisexualis* were inoculated at four equi-

distant locations near the periphery of a plate of lentil agar, with alternating ♂'s and ♀'s. Inoculum of the plant to be tested was placed in the center of the plate. After three to four days sufficient growth of all the mycelia had occurred to establish lines of intermingling between the unknown plant in the center and each



FIGS. 1, 2. *Achlya ambisexualis*, sexual strain predominant-female. 1, Portion of mycelium in single pure culture of two weeks. Oögonia and antheridia produced in small restricted areas, usually in the older parts of the mycelium near the substrate. $\times 37$. 2, Single oögonium and attached antheridia. Oösphere formation and fertilization occurred as in matings of compatible strains. $\times 200$.

of the four test plants. One to three additional days were sufficient to indicate the sexual affinities, compatibilities and strength of the previously unknown plant insofar as the reaction in matings with the sexual strains of the two test species could declare those qualities.

Gross water cultures of the isolates were maintained throughout and each was transferred to agar and freed of its contaminants as need for it arose. The technique previously described by the author (1937) was employed to secure bacteria-free mycelia.

EXPERIMENTAL STUDIES

From the first observation made on cultures of *A. ambisexualis* it was apparent that its various isolates and varieties offered exceedingly favorable material for a study of sexuality. Preliminary matings of the isolates showed that strong sexual reactions occurred in certain of the combinations. Apparent heterothallism in the species was thus established early in the work.

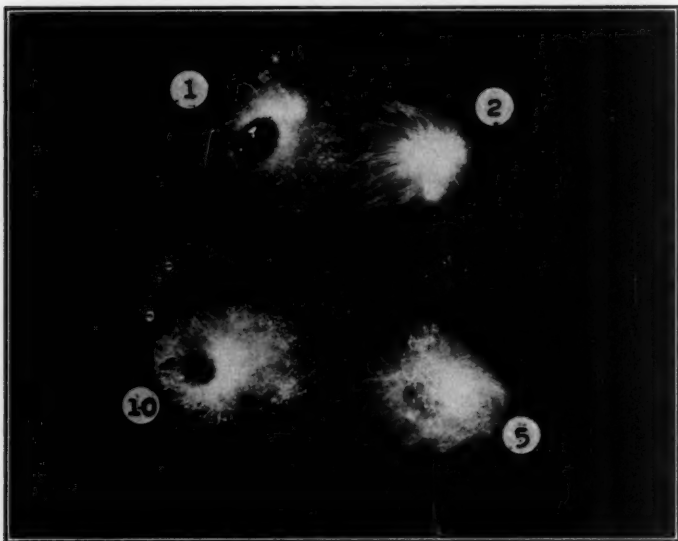


FIG. 3. Water mating of isolates 1 (pure ♂), 2 (predominant ♂), 5 (predominant ♀), and 10 (pure ♀). Four lines of sexual organs were produced as isolates 2 and 5 each reacted as ♂ and ♀ simultaneously. $\times 2$.

On fact, however, indicated that the sexual condition was more complicated than a strict separation of ♂ and ♀ potentialities in two different strains. While four of the 10 isolates remained sexually sterile in single culture, the usual behavior for the sexual strains of heterothallic organisms, the remaining six were weakly and spasmodically self-fertile (hermaphroditic). Single spore cultures of these isolates often produced a small number of oögonial initials in restricted areas 10–15 days after transfer (FIG. 1). In

these areas also developed declinous antheridial branches. These were attracted to the oogonial initials which underwent normal development with the formation of a small percentage of mature oöspores (FIG. 2). Those oogonial initials not reached by antheridial branches disintegrated. This situation differs in two respects from the production of ♂ and ♀ organs in a normal homothallic form: (1) here the sexual organs are not produced uniformly over the entire mycelium, and (2) they are not formed when the mycelium is at the height of its vegetative vigor. Although these plants are capable of giving a strong unisexual reaction when mated with certain other isolates, they exhibit only very feeble sexual potency after the hermaphroditic production of sexual organs. The same phenomenon has been described in *A. regularis* by Coker and Leitner (1938).

Matings of the ten isolates in all possible combinations made clear the inherent bisexual nature of the occasional hermaphroditic isolates. The results of these matings are given in table II.

Beyond indicating the combinations of isolates between which mating will occur the material embodied in table II brings out a number of interesting points that require further explanation. These include: (1) compatibilities, (2) sexual reversals, (3) grouping into sexual strains, and (4) intra-strain sterility and inter-strain fertility.

(1). Compatibilities: Each of the ten isolates mated with at least five of the others. Isolates 1 and 2 regularly gave reactions in all of the nine possible combinations for each. Isolates 8, 9, and 10 regularly mated in seven of the nine possible combinations while isolates 3-7 inclusive reacted in five of the possible nine contrasts for each. The fact that two of the isolates mated in all of their possible combinations indicated that at least one of them was reacting as both ♂ and ♀.

In all of the matings where a reaction was obtained there was nearly perfect compatibility with well over 90 per cent of the sexual organs produced reaching maturity and with normal oöspores matured in at least an equal percentage.

(2). Sexual reversals: Of the ten isolates used, six, 2-7 inclusive, behaved either as antheridial (♂) or oogonial (♀) mycelia depending on the predominant sexual character of the mate. Iso-

TABLE II

Isolates

Isolates		10	9	8	7	6	5	4	3	2	1
	1	III	III	III	III	IV	IV	III	I	I	
	2	IV	IV	IV	III	II	II	I	II		
	3	II	III	II	—	—	—	—			
	4	IV	IV	III	—	—	—				
	5	IV	IV	II	—	—					
	6	I	III	II	—						
	7	III	III	I							
	8	—	—								
	9	—									
	10										

Legend:

Isolates numbered 1-10 in order of increasing ♀ and decreasing ♂ potency

Therefore in each mating isolate with the higher number reacts as ♀

Roman numeral indicates relative strength of each reaction

Minus sign indicates no reaction

(Reactions in vertical columns ♀, in horizontal columns ♂)

late 2 exhibited strong ♂ reactions in eight of its nine combinations while in the ninth, with isolate 1, it reacted as a ♀ with the production of functional oögonia. Likewise isolates 3-7 produced oögonia when mated with isolates 1 and 2 and antheridia when contrasted with isolates 8, 9, and 10. The remaining isolates were strictly unisexual, isolate 1 reacted as ♂ in all combinations with other isolates and isolates 8, 9, and 10 reacted consistently as ♀.

(3). Grouping into sexual strains: From the data presented above it is possible to place the ten isolates of this species in four sexual strains, the members of each exhibiting identical sexual characters. These strains comprise (a) *pure male*, isolate 1; (b) *predominant male*, isolate 2; (c) *predominant female*, isolates 3-7 inclusive; and (d) *pure female*, isolates 8, 9, and 10.

(4). Intra-strain sterility and inter-strain fertility: No sexual reaction has ever been observed in matings of isolates belonging to the same sexual strain. All other combinations, however, lead to sexual reactions. *Pure male* reacts as ♂ to *predominant male*, *predominant female*, and *pure female*, the members of the latter strains reacting as ♀ in these crosses. Similarly *predominant male* reacts as ♂ to *predominant female* and *pure female*. Finally *predominant female* reacts as ♂ in matings with members of strain *pure female* (FIG. 4).

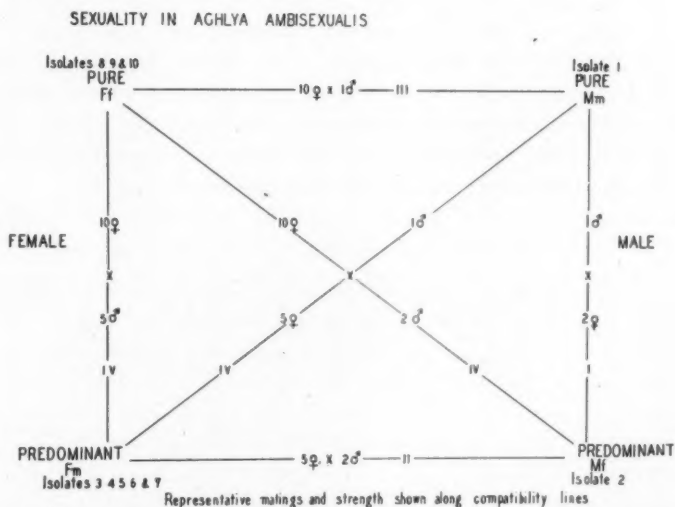


FIG. 4. Diagram of sexual strains in *Achlya ambisexualis* and the combinations in which matings occur. Along the lines are given representative matings, their relative strength, and the isolate in each reacting as ♂ and as ♀.

It is then apparent that all intra-strain combinations are sterile and all inter-strain combinations are fertile. Although the members of both *predominant male* and *predominant female* strains are occasionally hermaphroditic, the condition here cannot be compared with that found by Ames (1934) in the Ascomycete *Pleurage anserina*. In that species hermaphroditism was regular and constant with compatibility factors governing the ability of two mycelia to react reciprocally.

Further evidence of the bisexual character of isolates belonging to strains *predominant* ♂ and *predominant* ♀ is their behavior in simultaneous inter-strain matings. When isolates 1, 5, and 10 were mated simultaneously in water or on lentil-extract agar, three lines of sexual organs were formed with approximately the same number of oogonia in each line. Isolate 1 reacted as ♂ to both isolates 5 and 10; 10 reacted as ♀ to both 1 and 5; thus isolate 5 produced antheridia on the side toward 10 and oogonia in juxtaposition to the mycelium of isolate 1. The same type of simultaneous mating has been made for isolates 1, 2, 5, and 10 both on agar and in water. On semi-solid substrate only three lines of sexual organs have been produced, with isolate 2 reacting only in a ♂ capacity. In water matings, however, four lines of sexual organs have been seen (FIG. 3) with both isolates 2 and 5 behaving simultaneously as ♂ and ♀. Thus between the extremes of pure ♂ and pure ♀ there are at least two intergrades.

DISCUSSION

The sexuality of *Achlya ambisexualis*, like that of other members of the Saprolegniales previously described as heterothallic, differs markedly from that earlier described and defined as heterothallism by Blakeslee (1904). It is entirely possible that a single type of variation from the common heterothallic condition is the rule in this group of plants. In any event sufficient work has been done on these forms to signify that neither the term nor the definition of heterothallism is applicable to the condition encountered.

From the results of previous work and those of the present study it seems that there are six sexual strains with different sexual characters involved in this type of sexuality. These six strains may be expressed as all possible combinations of four sexual factors: *F*, dominant femaleness; *f*, latent femaleness; *m*, latent maleness; and *M*, dominant maleness. Thus the strains possible could be represented by the following formulae: (1) *FM*, hermaphroditic and self-fertile with both sexes strong and balanced; (2) *Ff*, pure female; (3) *Fm*, predominant-female with male potentialities; (4) *Mf*, predominant-male with female potentialities; (5) *Mm*, pure male, and finally, (6) *fm*, sexually sterile, both sexes weak and

balanced. This grouping of the sexual strains was suggested by Bishop in his doctorate thesis (1937) on sexuality in *Sapromyces Reinschii*, in which species he found three of these strains, *Fm*, *Mm*, and *mf*.

These formulae as applied here express the sexual characters of the plants of the various strains. No implications of genetic combinations or constitution are intended.

Two of these six strains, *Ff*, and *Mm*, are comparable to the ♂ and ♀ strains encountered in strict heterothallic forms. These are constantly sexually sterile in single culture; male and female reproductive organs are formed by them only when they are brought together. The two strains in which one or the other sex is predominant, *Fm* and *Mf*, differ from the former by (1) the spontaneous production in single culture of a relatively small number of male and female sexual organs which in most of the cases reported, fail to develop to maturity and (2) the ability of these strains, when crossed with pure ♂, pure ♀, or the opposed predominantly sexed plant, to give a reaction opposite that of the predominant sexual potency of the mate. For instance, it has been shown above that strain *Fm*, isolate 5, of *A. ambisexualis* will react as a ♀ to both *Mm*, isolate 1 pure male, and *Mf*, isolate 2, predominant-male but will react as a ♂ to strain *Ff*, isolate 10, pure female. Figure 4 schematically represents these sexual strains and their inter-reactions in *A. ambisexualis*.

The hermaphroditic self fertile strain, *FM*, corresponds in its behavior to the forms ordinarily termed homothallic in this and other groups. Finally, the sterile strain, *fm*, is devoid of sexual expression and reproduces only by asexual and vegetative means. Neither the homothallic nor the sexually sterile strain is represented among the isolates of *A. ambisexualis*.

The differences between heterothallism, as defined by Blakeslee (1904), and the sexuality in *A. ambisexualis*, as well as in *A. bisexualis*, *Dictyuchus monosporus*, and *Sapromyces Reinschii* necessitates the introduction of a term more exactly descriptive of the sexual condition of these water molds. To fill this need the writer in connection with the description of *A. ambisexualis* (1939) suggested the terms *gynandromixis* or *gynandromictic sexuality*, implying the mixed sexual character of the various strains

and the capacity of certain of these strains to react as ♂ or ♀ or both.

In the following table a listing of the occurrence of these various strains in the three gynandromictic species which have previously been thoroughly investigated is given in addition to those first described here for *A. ambisexualis*:

TABLE III

Species.....	<i>Dictyuchus monosporus</i> Couch	<i>Sapromyces Reinschii</i> Bishop	<i>Achlya bisexualis</i> Raper	<i>Achlya ambisexualis</i>
Investigator.....				
<i>FM</i>	×		× ³	
<i>Mm</i>	×	×	×	×
<i>Mf</i>	× ²		×	×
<i>Fm</i>	×	×	×	×
<i>Ff</i>	×		×	×
<i>fm</i>	×	×	×	

² Certain of Couch's isolates, made from germinated eggs, gave a ♂ or a ♀ reaction when mated with strong ♀ or ♂ respectively, but each was apparently either predominantly ♂ or predominantly ♀. Although these plants were not observed to produce antheridia and oögonia in single culture, it seems that their inclusion in these groups is entirely logical.

In addition to the six strains listed above, Couch found one which was characteristically parthenogenetic but capable of producing antheridial hyphae when crossed with a strong ♀ plant, although it showed no reaction when mated with a strong ♂.

³ Descriptions of these strains as yet unpublished.

A similar condition is indicated in at least two species of the Peronosporales. Leonian (1931) showed that homothallic, ♂, ♀, and neuter strains were involved in *Phytophthora omnivora*. He suggested that some or all of the strains probably contained potentialities for both sexes; his results, however, clearly indicate bisexuality only in the homothallic strain. Bruyn (1935, 1937) demonstrated a comparable condition in the obligate parasite *Peronospora parasitica*. In that species were found strains which were homothallic, unisexual (two of these, ♂ and ♀ unidentified because of the growth habit of the fungus), and one which was predominantly of one sex, yet capable of occasional sexual reversals and self-fertility. It does not seem unlikely that the same type of sexuality is common to both the Saprolegniales and the Peronosporales.

Relative sexuality has been shown in the work on *A. ambisexualis* perhaps as strikingly as anywhere in the fungi, for of ten isolates of that species, six are capable of reacting as either ♂ or ♀.

Can such reversals and the entire sexual condition be elucidated by the scheme of Hartmann (1925-31) explaining the bisexuality of gametes and the phenomenon of relative sexuality? The theory of relative sexuality as promulgated by Hartmann holds that the gametes (and indeed all other cells of the organism) contain an inherent factor for each sex and that gametes are capable of sex reversibilities depending on the internal and external environmental conditions. His explanation for these phenomena in haplonts such as *Ectocarpus* and a majority of the Thallophytes postulates the presence of both sex potentialities, ♂ and ♀, of equal strength in the zygote or sporophytic generation. In meiosis at the initiation of the gametophytic generation one of these sex potentialities is developed at the expense of the other without, however, rendering it incapable of expression. Such a condition existing in gametes would allow them to behave as unisexual under normal circumstances but when mated with stronger gametes of the same sex would allow their copulation in the opposite capacity. This ability for sex reversibility has been demonstrated in a large number of algae and a few fungi.

This scheme of Hartmann's was originally postulated to apply to those organisms in which ultimate sex determination is dependent on the environmental conditions in the broadest sense. Such sex determination is known as haplophenotypic. Later, however, this concept has been extended to those plants in which final sex determination occurs at the time of meiosis. These are termed haplogenotypic types. *Dictyuchus* belongs to the latter group according to Kniep (1928) and Hartmann (1931). Since the sexuality found in the other water molds that are not strictly hermaphroditic and self fertile (homothallic in the classical sense) is essentially like that found in *Dictyuchus*, it may safely be assumed that sexual differentiation in such forms is also genotypically determined. Of course in such forms the worker is not concerned with sexual reversability in the gametes themselves but in the entire mycelia. That is to say, in addition to primary sex characters (behavior of gametes in copulation) as shown in *Ectocarpus*, the

water molds show marked and characteristic secondary sex characters and it is mainly these with which investigators in the aquatic Phycomycetes must deal.

Since the production of gametes is not immediately preceded by meiotic divisions, the mycelium necessarily has nuclei with the same potentialities and components as the gametes. The possibility of the presence of nuclei of different components in the mycelium is strongly opposed by the stability of the sexual characters of the plants over a long period of time and through a number of single-spore generations.

If only the predominantly sexed plants had been found there would be complete agreement between the situation found here and that postulated by Hartmann, but when the entire complex involved is considered there are discrepancies which are significant. Isolates belonging to the ♀ strains, *Ff* and *Fm*, show quantitative differences of the female valence as would be expected from his hypothesis, and that some of the plants are capable of sexual relativity. But in addition to these rather gradual variations of sexual potency or valence, there are constant qualitative differences. These qualitative differences are the points on which the two strains are separated, namely, the ability of the latter to produce sexual organs in single culture and their behavior in inter-strain matings. If there were gradual transitional stages between the two strains, they could be explained on the relative strength of the latent potency, or at least the varying balance between the predominant and the latent potentialities. No such transitional stages have been recorded in any of the gynandromictic water molds. In addition to the two strains which obviously have both ♂ and ♀ potentialities, *Fm* and *Mf*, the work done on this group to date indicates that there are two pure unisexual strains, *Ff*, and *Mm*, in which there are apparently no factors allowing for sexual reversibility. In all of the forms studied such pure strains have constantly given only a single reaction in spite of having been mated in all possible combinations with other strains. The possibility that these so-called pure strains have the potentialities of both maleness and femaleness, one very powerful and the other exceedingly impotent in each, must not be overlooked; the points here considered as extremes may be relative rather than absolute. But if this were

the case, why are these alleged pure ♂ and pure ♀ strains so constantly sterile in single culture while only those that have been shown capable of both sexual reactions produce sexual organs of both sexes spontaneously? And why the sharp line of demarcation between them?

Consideration of these points and the additional evidence furnished by the hermaphroditic self-fertile (*FM*) and the sterile (*fm*) strains shows that the complex sexuality of these water molds cannot be explained simply on the basis of Hartmann's theory of relative sexuality. The sexuality of these forms, so far as the facts are now known, can be adequately explained by a modified scheme similar to that suggested by Hartmann (1929) and Vandendries (1930) for tetrapolar Hymenomycetes. Complete understanding of the process through which the different strains arise and are perpetuated in nature, however, will depend on further studies on oöspore germination. Although oöspores of *Dictyuchus monosporus* Couch (1926) and *Achlya ambisexualis* have been germinated and the progeny tested for sexuality, the limited data from these two cases only serve to emphasize the complex nature of the sexuality in these forms. A genetic study of the progeny of crosses between the strains of *A. ambisexualis* (six different contrasts) is being carried on by the writer.

SUMMARY

A study of sexuality in *A. ambisexualis* shows that four sexual strains are represented among the isolates of that species: (1) pure ♂, (2) predominant ♂, (3) predominant ♀, and (4) pure ♀. These strains are cross-fertile in all combinations. Plants of the two predominantly sexual strains are weakly self-fertile, and give either a ♂ or a ♀ reaction when mated, depending on the stronger sexual affinity of the mate. Plants of both predominant ♂ and ♀ strains have been shown capable of reacting simultaneously as ♂ and ♀ in different portions of their thalli. In this species sexual reversals are shown as strikingly as anywhere in the fungi.

The six sexual strains found in the various so-called heterothallic species may be expressed as all possible combinations of four sexual factors: *M*, dominant maleness; *m*, latent maleness;

f, latent femaleness; and *F*, dominant femaleness. The combinations possible are: *Mm*, pure ♂; *Mf*, predominant ♂, but also capable of reacting as ♀; *Fm*, predominant ♀, capable of reacting as ♂; *Ff*, pure ♀; *FM*, homothallic, both sexes strong and balanced; and *fm*, sexually sterile, both sexes weak and balanced.

To differentiate this sexual situation from heterothallism as defined by Blakeslee, the term *gynandromixis* or *gynandromictic sexuality* has been suggested, implying the mixed sexual characters of the thalli of the various strains and the capacity of two of these strains to behave as ♂ and/or ♀.

LITERATURE CITED

- Ames, L. M. Hermaphroditism involving self-sterility and cross-fertility in the Ascomycete *Pleurage anserina*. *Mycologia* 26: 392-414. 1934.
- Bishop, H. A study of sexuality in *Sapromyces Reinschii*. Ph.D. Thesis, Harvard University, Cambridge (unpublished).⁴ 1937.
- Blakeslee, A. F. Sexual reproduction in the Mucorinae. *Proc. Am. Acad.* 40: 205-319. 1904.
- Bruyn, Helena L. G. de. Heterothallism in *Peronospora parasitica*. *Phytopath.* 25: 8. 1935.
- . Heterothallism in *Peronospora parasitica*. *Genetica* 19: 553-558. 1937.
- Burgeff, H. Über Sexualität Variabilität und Vererbung bei *Phycomyces nitens*. *Ber. Deuts. Bot. Ges.* 30: 679-685. 1912.
- Coker, W. C. Other water molds from the soil. *Jour. Elisha Mitchell Sci. Soc.* 42: 207-226. 1927.
- and Leitner, J. New species of *Achlya* and *Apodachlya*. *Jour. Elisha Mitchell Sci. Soc.* 54: 311-318. 1938.
- Couch, J. N. Heterothallism in *Dictyuchus*, a genus of the water molds. *Ann. Bot.* 40: 848-881. 1926.
- Hartmann, M. Untersuchungen über relative Sexualität. *Biol. Zentralbl.* 45: 449-467. 1925.
- . Verteilung, Bestimmung, und Vererbung des Geschlechts bei den Protisten und Thallophyten. In Baur & Hartmann *Handbuch der Vererbungswissenschaft* 2E: 1-115. 1929.
- . Relative Sexualität und ihre Bedeutung für eine allgemeine Sexualität- und eine allgemeine Befruchtungstheorie. *Naturwissensch.* 19: 8-16, 31-37. 1931.
- Kniep, H. Die Sexualität der Niederen Pflanzen. Fischer, Jena. 1928.
- Leonian, L. H. Heterothallism in *Phytophthora*. *Phytopath.* 21: 941-955. 1931.
- Raper, J. R. Heterothallism and sterility in *Achlya* and observations of the cytology of *Achlya bisexualis*. *Jour. Elisha Mitchell Sci. Soc.* 52: 274-289. 1936.

⁴ *Mycologia* 32: 505-529. 1940.

- , A method of freeing fungi from bacterial contamination. *Science* **85**: 342. 1937.
- , Sexual hormones in *Achlya*. I. Indicative evidence for a hormonal coördinating mechanism. *Am. Jour. Bot.* **26**: 639-650. 1939.
- Vandendries, R.** La conduite sexuelle des Hymenomycetes interpretée par les theories de Hartmann concernant le bisexualité et la relativité sexuelle. *Bull. Acad. Belg. V.* **16**: 1213-1234. 1930.
- Weston, W. H., Jr.** Heterothallism in *Sapromyces Reinschii*. Preliminary note. *Mycologia* **30**: 245-253. 1938.

SOME NEW SPECIES OF ASCOMYCETES ON CONIFEROUS HOSTS

EDITH K. CASH AND ROSS W. DAVIDSON

(WITH 2 FIGURES)

The fungi here described include one pyrenomycete and four discomycetes collected on conifers in various localities of the United States. Specimens cited are deposited in the Mycological Collections of the Bureau of Plant Industry; type material of the *Cenangium* has also been sent to the herbaria of the New York Botanical Garden and the University of Michigan and to the Farlow Herbarium of Harvard University.

1. *Acanthonitschkea coloradensis* sp. nov. (FIG. 1, E, F)

Perithecia emerging from the bark in closely packed clusters of 10-50 from a common stroma 1-2 mm. diam., carbonaceous, subglobose to turbinate or pyriform, or contorted by mutual pressure, then collapsing and disciform, black, dull or shining, setose, 200-300 μ diam., wall 25-50 μ thick, with circular ostiole 12-15 μ in diam.; asci cylindrical, apex narrowed and truncate, 70-75 \times 4-5 μ ; spores hyaline, one-celled, 2-guttulate to pseudoseptate, broad-ellipsoid, obliquely uniseriate, 6-8 \times 3-4 μ ; paraphyses not seen; setae numerous, dark-brown, rigid, short and thick, 15-40 (55) μ long, 7-9 μ thick at the base; stromatic tissue of loosely interwoven, brown hyphae 2-3 μ thick, becoming more dense and darker at the base of the perithecia; perithecial walls of several layers of thin-walled, brown pseudoparenchyma, dense and black toward the cortex, subhyaline toward the perithecial cavity.

Peritheciis 10-50 in stromate singulo, 1-2 mm. diam. emergenti conglobatis, carbonaceis, subglobosis vel turbinatis, atris, setosis, 200-300 μ diam., circulariter ostiolatis; ascis cylindricis, apice angustato et truncato, 70-75 \times 4-5 μ ; ascosporis hyalinis, unicellularibus, pseudoseptatis, late ellipsoideis, 6-8 \times 3-4 μ ; setis numerosis, atrobrunneis, rigidis, 15-40 (55) \times 7-9 μ .

On dead twig of *Abies lasiocarpa* (Hooker) Nuttall, Mesa Lakes, Grand Mesa, Colo., June 1, 1938, R. W. Davidson, F. P. 71992.¹

¹ "F.P." numbers are those of the Division of Forest Pathology; "Myc. Coll.," the Mycological Collections of the Bureau of Plant Industry.

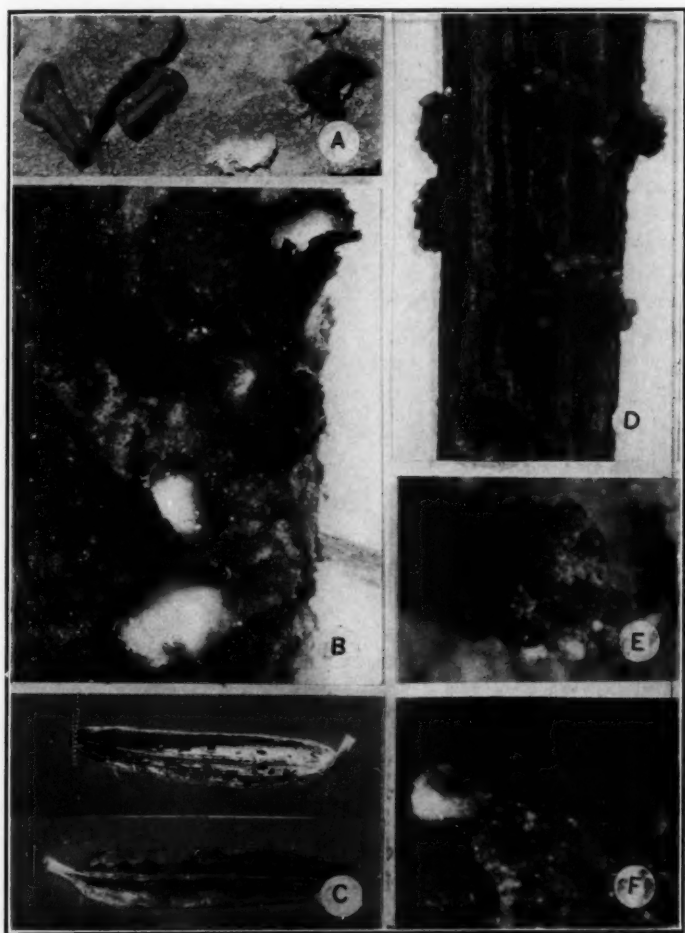


FIG. 1. A, B, *Cenangium atropurpureum* on *Pinus nigra*, $\times 7$; C, *Phacidium Tsugae* on *Tsuga canadensis*, $\times 5$; D, *Mollisia Scoleconectriae* on *Scoleconectria scolecospora* on *Pinus Strobus*, $\times 8$; E, F, *Acanthonitschkea coloradensis* and *Dasyscypha Acanthonitschkeae* on *Abies lasiocarpa*, E $\times 20$; F $\times 50$. (Photographic negatives by M. L. F. Foubert.)

The conidial stage in culture from single ascospores is of the *Cephalosporium* type; cultures after 3 months development on 2.5 per cent malt agar at 11° C. strawberry-pink;² hyphae hyaline; conidiophores $12-35 \times 3-5 \mu$; conidia hyaline (pink in mass), $2-5 \times 1-1.6 \mu$.

In general structure this fungus seems most closely related to *Nitschkia* Otth. from which it differs in the spiny perithecia. Of the three genera in the Nitschkeae having setose perithecia, *Fracchiaca* Sacc. (7) has polysporous asci, and *Fitzpatrickia* Ciferri (1, p. 29) brown spores; the Colorado fungus is therefore referred to *Acanthonitschkea* Speg., with which it agrees in the turbinate, collapsing, setose perithecia, the eight-spored asci and the hyaline spores. Both of the two species previously described in this genus are American, *A. argentinensis* Speg. occurring in Puerto Rico and Argentina, and *A. macrobarbata* Fitzpatrick in the West Indies (6, p. 62-64). The Colorado species may be distinguished by shorter spines, longer asci, and more sharply delimited stromata with fewer perithecia present on each stroma. The spores of *A. coloradensis* resemble those of *A. macrobarbata* in form, rather than the allantoid spores of *A. argentinensis*. Iridescent mycelium noted as a character of the other two species was not observed in *A. coloradensis*, although old perithecia from which setae have been rubbed off occasionally show traces of iridescence.

2. *Dasyscypha Acanthonitschkeae* sp. nov. (FIG. 1, E, F)

Apothecia scattered, 1-8 on a single stroma of *Acanthonitschkea coloradensis*, sessile, nearly globose at first, then cup-shaped to subglobose, with circular opening, fleshy-waxy, white, 0.1-0.2 mm. in diameter and height, margin and exterior white-tomentose, hymenium translucent-white; asci cylindrical, rounded at the apex, 8-spored, $22-24 \times 3-3.5 \mu$; spores uniseriate, hyaline, one-celled, ellipsoid, $3.5-4 \times 1.5-2 \mu$; paraphyses filiform, hyaline, unbranched, not enlarged at the tips; exciple hyaline, prosenchymatous; hairs hyaline, septate, not swollen at the apex, thickly incrustated and verrucose, $65-90 \times 3-4 \mu$.

Apotheciis sessilibus, globosis dein cupulatis, carneo-ceraceis, albis, 0.1-0.2 mm. diam. et altis, margine et extus albo-tomentosis, hymenio aquoso-albo;

² Color nomenclature throughout is that of Ridgway, R., Color standards and color nomenclature. Washington, 1912.

ascis cylindricis, apice rotundatis, octosporis, $22-24 \times 3-3.5 \mu$; sporis uniseriatis, hyalinis, unicellularibus, ellipsoideis, $3.5-4 \times 1.5-2 \mu$; paraphysibus filiformibus, hyalinis; pilis hyalinis, septatis, incrustatis, $65-90 \times 3-4 \mu$.

On stromata of *Acanthonitschkea coloradensis* Cash & Davidson on *Abies lasiocarpa* (Hooker) Nuttall, Mesa Lakes, Grand Mesa, Colorado, June 1, 1938, R. W. Davidsion, F. P. 71992-a.

The only *Dasyscypha* species described as occurring on pyrenomycetes is *D. episphaeria* (Mart.) Rehm, in which the dimensions of asci and spores are not recorded; however, it differs from the Colorado fungus in the color of the hymenium. Other species of *Dasyscypha* with small asci and spores which are reported on coniferous hosts differ also in color and in the presence of a stipe.

3. *Phacidium Tsugae* sp. nov. (FIG. 1, C; 2)

Apothecia hypophyllous, subepidermal, then exposed by the circumscissile removal of the epidermis and widely expanded, broad-elliptical to orbicular in outline, honey yellow to isabella color when moist, drying nearly black, $150-275 \mu$ in diam., 100μ in depth; asci

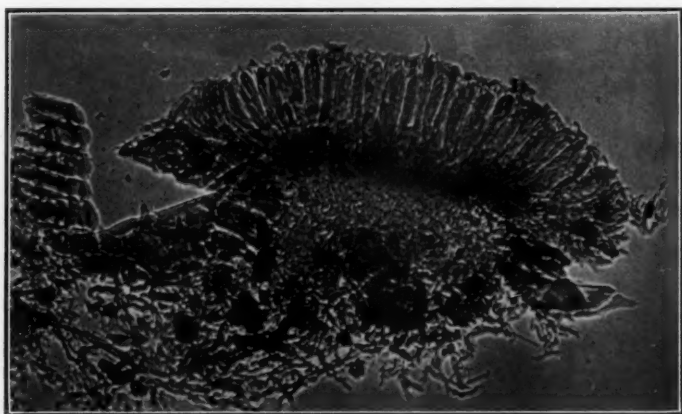


FIG. 2. *Phacidium Tsugae*, section of apothecium, \times about 300. (Photographic negatives by M. L. F. Foubert.)

broad-clavate or subfusoid, narrowing abruptly to a short stipe, broadly rounded at the apex, 8-spored, $50-65 \times 15-18 \mu$; spores irregularly and obliquely crowded, one-celled, hyaline, ellipsoid with

obtuse ends, straight or slightly curved, granulose, $18-22 \times 5-7 \mu$; paraphyses filiform, branched and recurved at the tips, with a yellowish mucilaginous coating which joins the tips in a mazaedium; hypothecium $50-60 \mu$ thick, composed of a dense, pale brownish layer 20μ thick immediately below the ascus layer, and an underlying and more loosely interwoven layer $30-40 \mu$ deep extending into the leaf tissue.

Apotheciis hypophyllis, subepidermicis, epidermide orbiculatim scindenti et hymenium flavidum patefacienti, dein expansis et disciformibus, $150-275 \mu$ diam., 100μ altis, siccis nigris; ascis late-clavatis vel subfusoides, abrupte in stipitem brevem attenuatis, apice rotundatis, octosporis, $50-65 \times 15-18 \mu$; ascosporis irregulariter et obliquiter confertis, unicellularibus, hyalinis, ellipsoideo-oblongis, granulosis, $18-22 \times 5-7 \mu$; paraphysibus filiformibus, apice ramosis et recurvatis, in mazaedium flavidulum conglutinatis; hypothecio subhyalino, $50-60 \mu$ crasso.

On discolored needles of *Tsuga canadensis* (L.) Can., Pineola, N. Car., E. R. Toole, June 24, 1938, F. P. 72022, associated with *Keithia Tsugae* (Farl.) Durand.

A few brownish, pseudo-septate spores, similar to the ascospores in shape and size, were observed embedded in the mazaedium, but none were found in the asci. Their connection with the fungus is doubtful, and, since the spores found in the asci are simple and hyaline, it is described as a species of *Phacidium*. Dearness (3, p. 237) reports occasional septate spores in *P. infestans* Karst.

Tsuga is listed by Faull (4, p. 32; 5, p. 139) among the various genera of conifers attacked by the snow cover *Phacidium* blight caused by *P. infestans*. *P. Tsugae* resembles this species and its variety, *P. infestans* var. *Abietis* (3, p. 237), in the dimensions of the asci and spores, but is distinctly different in the manner of opening and the scattered occurrence on the needles as contrasted with the linear arrangement of *P. infestans*. The widely expanded apothecia are similar to those in *P. expansum* Davis on *Picea Mariana* (2, p. 424, pl. 32) and the circumscissile splitting of the epidermis is like that of *P. Balsameae* Davis (l.c.) on *Abies balsamea*; both of these species, however, have shorter spores. The opening by a circular lid is a character of the genus *Stegopezizella* Sydow (9, p. 293-394), based on *Phacidium Balsameae*; however, a surrounding wall of parallel, black hyphae such as that described for *P. Balsameae* is lacking in the species on hemlock. Differences

from these and other species of *Phacidium* on conifer needles indicate that the fungus has hitherto not been described.

4. **Mollisia Scoleconectriæ** sp. nov. (FIG. 1, D)

Apothecia caespitose on and sometimes completely covering stromata and perithecia of *Scoleconectria scolecospora*, 0.2–0.4 mm. in diam., fuscous black, sessile, soft fleshy, globose with small circular opening, then cupulate, hymenium dark olive gray, margin fimbriate, incurved when dry; asci cylindrical-clavate, with apex broadly rounded, 8-spored, $25\text{--}35 \times 3\text{--}4 \mu$; spores biseriata, hyaline, unicellular, narrow-cylindrical, straight or slightly curved, $5\text{--}7 \times 1 \mu$; paraphyses filiform, hyaline, unbranched, 1μ in diameter; hypothecium hyaline, prosenchymatic, about 25μ thick; exciple brown, pseudoparenchymatic at the base, gradually changing into free, hyaline hyphae at the fimbriate margin.

Apotheciis in stromatibus et peritheciis *Scoleconectriæ scolecosporae* dense caespitosis, 0.2–0.4 mm. diam., atro-brunneis, nigrescentibus, sessilibus, globosis, cupulatis, hymenio cinereo, margine fimbriato; ascis cylindricis, apice late rotundatis, octosporis, $25\text{--}35 \times 3\text{--}4 \mu$; sporis biseriatis, anguste cylindricis, hyalinis, continuis, rectis vel leniter curvatis, $5\text{--}7 \times 1 \mu$; paraphysibus filiformibus, hyalinis, non ramosis, 1μ diam.; contextu excipuli basi pseudoparenchymatico, marginem versus hyphas elongatas, hyalinas exeunte.

On stromata of *Scoleconectria scolecospora* (Bref.) Seaver on twigs of *Pinus Strobus* L. near Stone Creek, Huntingdon Co., Pa., Feb. 19, 1933, L. O. Overholts and R. W. Davidson, F. P. 86440 (*type*), near State College, Pa., L. O. O. and R. W. D., Apr. 27, 1940, F. P. 86479, and Norwich, N. Y., Apr. 25, 1933, R. W. D., F. P. 86445.

Macroscopic examination of herbarium specimens of *Scoleconectria* has failed to show the presence of this *Mollisia*; however, it may easily have been overlooked, since the small and inconspicuous apothecia might readily be mistaken for old darkened perithecia of the host fungus. This species is distinct from all of the dozen or more species of *Mollisia* found on *Pinus*, both in its occurrence on *Scoleconectria* and in its morphology, particularly in its narrow spores.

5. *Cenangium atropurpureum* sp. nov. (FIG. 1, A-B)

Apothecia 2-5 mm. in diam. and height, erumpent singly or two or three together from stroma beneath the bark, subglobose then cupulate, fleshy-leathery, substipitate, exterior furfuraceous, dull purplish black to fuscous black when moist, raisin black when dry; margin lacerate, becoming inrolled when dry and apothecia triangular or hysteroïd; hymenium light ochraceous buff to chamois colored; asci cylindrical, apex flattened with pore usually toward one side, 8-spored, $70-85 \times 9-12 \mu$; spores broad-ellipsoid, irregularly uniseriate, hyaline, one-celled, containing several small scattered guttules, $9.5-11 \times 5-8 \mu$; paraphyses hyaline, unbranched, enlarged at the apex to $3-5 \mu$; hypothecium $20-30 \mu$ thick, prosenchymatic, pale brownish; intermediate layer plectenchymatic, $100-150 \mu$ thick, of hyaline, thick hyphae; cortex $100-200 \mu$ thick, black, dense, furrowed and lacerate on the surface.

Apotheciis 2-5 mm. diam. et altis, erumpentibus, subglobosis dein cupulatis, carneo-coriaceis, furfuraceis, atropurpureis, margine lacerato, hymenio ochraceo; ascis cylindricis, octosporis, $70-85 \times 9-12 \mu$; sporis late ellipsoideis, hyalinis, unicellularibus, guttulatis, $9.5-11 \times 5-8 \mu$; paraphysibus hyalinis, simplicibus, apice usque $3-5 \mu$ inflatis; hypothecio pallide brunneo; cortice atro, lacerato.

On dead twigs of *Pinus nigra* Arnold, Sugar Loaf Mt., Md., Apr. 25, 1935, R. W. Davidson and M. E. Fowler, F. Path. 59167 (type); *P. Mugo* Turra, *P. pungens* Lambert, *P. rigida* Miller, and *P. virginiana* Miller, Maryland; *P. taeda* L., Georgia; *P. sylvestris* L., Pennsylvania, in Herb. L. O. Overholts 15611.

In the dimensions of the asci and spores this *Cenangium* is close to *C. Abietis* (Pers.) Rehm, common on various coniferous hosts. The apothecia, however, are larger than is usual in the latter species, which Schwarz (8, p. 47) reports as 1.5-2.5, rarely 3 mm., in diameter. The purplish color is a feature not noted for *C. Abietis* or other species of *Cenangium* described on conifers.

No conidia have been observed on the twigs or in pure cultures grown on 2.5 per cent malt agar. The mycelium in culture is not as dark as is the mycelium of *C. Abietis* from *Pinus ponderosa* Lawson, which on the same medium produced an abundance of conidia.

BUREAU OF PLANT INDUSTRY,
WASHINGTON, D. C.

LITERATURE CITED

1. Ciferri, R. A new genus of the subfamily Nitschkieae. *Mycologia* 20: 29-30. 1 fig. 1928.
2. Davis, J. J. Notes on parasitic fungi in Wisconsin—VIII. *Trans. Wis. Acad.* 20: 413-431. *pl.* 31-32. 1921.
3. Dearness, J. New and noteworthy fungi—IV. *Mycologia* 18: 236-255. 1926.
4. Faull, J. H. Studies being made and progress in control of forest diseases. A fungus disease of conifers related to the snow cover. *Forestry Chronicle* 52: 29-34. 1929.
5. —. The spread and the control of *Phacidium* blight in spruce plantations. *Jour. Arnold Arboretum* 11: 136-147. 1930.
6. Fitzpatrick, H. M. Monograph of the Nitschkieae. *Mycologia* 15: 23-67. *pl.* 1-7. 1923.
7. —. The genus *Fracchiaca*. *Mycologia* 16: 101-114. *pl.* 10. 1924.
8. Schwarz, F. Die Erkrankung der Kiefern durch *Cenangium Abietis*. Beitrag zur Geschichte einer Pilzepidemie. 2 *pl.* Jena. 1895.
9. Sydow, H. & Petrak, F. Zweiter Beitrag zur Kenntnis der Pilzflora Nordamerikas, insbesondere der nordwestlichen Staaten. *Ann. Myc.* 22: 387-409. 1924.

SOME DERMATEA SPECIES AND THEIR CONIDIAL STAGES¹

J. WALTON GROVES²

(WITH 13 FIGURES)

The genus *Dermatea* is characterized principally by the dark colored, leathery apothecia occurring on twigs and branches of woody plants, ellipsoid to ellipsoid-fusiform ascospores, and the presence of a definite epithecium. The conidial stages of *Dermatea* species are usually referred to the form genus *Micropera*, which typically consists of a waxy-fleshy stroma containing one to several cavities bearing elongate-fusiform to sub-filiform conidia. Tulasne (1865) first drew attention to the association of *Micropera* species with *Dermatea* species, and observed the two stages arising from the same basal stroma. This association has also been noted by von Höhnelt (1916), Nannfeldt (1932), Seaver and Velasquez (1933), and others. The genetic connection has been generally accepted, although definite proof based on cultural studies has been lacking for the most part.

The species described in this paper were collected chiefly in the Temagami Forest Reserve, Ontario, and in the vicinity of Toronto, Ontario. Cultures were obtained from both ascospores and conidia and were grown on two per cent malt extract agar and on sterilized twigs of the host. The cultures from ascospores and conidia were similar in appearance and both produced the same conidial stage in culture. This was considered proof of genetic connection.

DERMATEA MOLLUSCULA (Schw.) Cash, Mycologia 29: 304. 1937.
Cenangium mollusculum Schw. Trans. Am. Phil. Soc. II. 4:
239. 1832.

¹ Contribution No. 615 from the Division of Botany and Plant Pathology, Science Service, Department of Agriculture, Ottawa, Canada. Part of the work was done at the Department of Botany, University of Toronto, and was included in a thesis presented to the School of Graduate Studies of that University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

² Graduate Assistant, Central Laboratory, Ottawa.

Gelatinosporium fulvum Peck, Ann. Rep. N. Y. State Mus. 38: 97. 1885.

A description of this species based partly on the writer's material was recently published by Miss Cash (1937) and it seems unnecessary to re-describe it now. It occurs on *Betula* species,

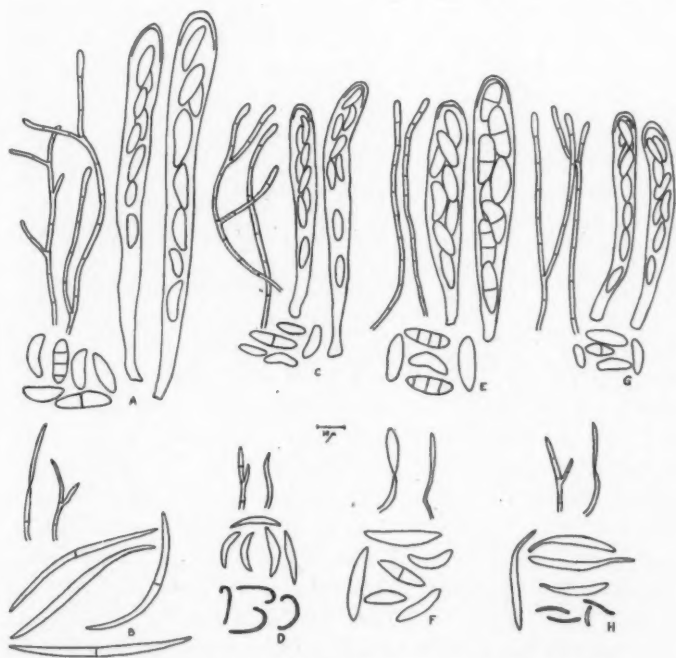


FIG. 1. A, B, *Dermatea molliuscula*; C, D, *D. Arieae*; E, F, *D. Hamamelidis*; G, H, *D. Viburni*.

apparently most commonly on *B. lutea* Michx. The specimens examined in this study are listed below.

SPECIMENS EXAMINED: University of Toronto Herbarium. On *Betula lutea*. 3525 (46),³ 8430 (193), Temagami Forest Reserve, Ontario—6773 (278), south of Aurora, Ontario.

³ The numbers in parentheses refer to duplicate specimens in the herbarium of J. W. Groves.

Mycological Herbarium, Science Service, Department of Agriculture, Ottawa, Ont. On *Betula lutea*. 3917, Chelsea, Que.—3918, Burnet, Que.—4694 (552), North Halton, Nova Scotia—5317 (599), Duchesnay, Que. On *B. papyrifera*. 2595 (440), Chelsea, Que.

Herbarium of J. W. Groves. On *Betula lutea*. 186, Temagami Forest Reserve, Ont. On *Betula* sp. 514, Colch. Co., Nova Scotia, ex herb. L. E. Wehmeyer 1287a—532, Holl Pond, N. Y., ex herb. Univ. of Michigan, Coll. C. H. Kauffman and E. B. Mains, Aug. 24, 1914—656, Lycoming Co., Penn., ex herb. L. O. Overholts 21611.

Ex Herbarium N. Y. Bot. Garden, unnumbered, Randolph, N. H. June 22, 1927 (as *Dermatea Betulae* Rehm).

Durand Herbarium. 3933, ex herb. Schweinitz, marked part of type.

On malt extract agar the colonies reach a diameter of 3–3.5 cm. in four weeks. They are whitish at first, then variously colored and more or less zoned with shades of olive, yellow, green, or brown, darker in the centre, the aerial mycelium short, even, and velvety. The conidial stromata are usually almost globose, up to 5 mm. in diameter, downy to velvety, whitish, buff, or yellowish, usually containing several lobed cavities which tear open irregularly. The tissue is composed of closely interwoven, hyaline hyphae about $2.5\text{--}4.0\ \mu$ in diameter, looser at the outside. The conidiophores are hyaline, cylindric, septate, branched, $1.5\text{--}2.0\ \mu$ in diameter, mostly $15\text{--}30\ \mu$ in length, sometimes longer, tapering to a fine point. The conidia are hyaline to pale yellowish, sub-filiform, sickle-shaped or sigmoid to almost straight, ends pointed, one to four celled, $50\text{--}75 \times 2.5\text{--}3.5\ \mu$. No microconidia have been observed.

On twigs of *Betula* very little aerial mycelium is produced, sometimes a few whitish to buff or grayish-brown tufts appear at the point of inoculation. The conidial stromata are strongly erumpent, rounded, sub-globose or slightly elongated, up to 4 mm. in diameter and 2 mm. in height, whitish to buff, yellowish, olivaceous, or brownish, covered with a short, downy mycelium. The structure is very similar to fruiting bodies of *Gelatinosporium fulvum* as found in nature.

This species is characterized chiefly by its occurrence on *Betula*, the strongly erumpent, often laterally fused apothecia, the long asci, and the type of conidial stage. It was first described by Schweinitz (1832) as *Cenangium molliusculum*, and transferred to *Dermatea* by Cash (1937).

This fungus was described and figured by Seaver and Velasquez (1933) who erroneously identified it as *Dermatea Betulae* Rehm. Dr. Seaver kindly sent a specimen of their fungus for examination and it is unquestionably *D. molliuscula*. *D. Betulae*, which was described by Rehm (1896), is a *Pezicula* and was subsequently transferred to that genus by Rehm (1912). The type of *D. Betulae* Rehm was collected and distributed by Sydow in Myc. March. 4359, and another specimen also collected by Sydow was distributed in Syd. Myc. Germ. 2165. Both of these specimens have been examined and are a *Pezicula* and quite distinct from *D. molliuscula*.

Seaver and Velasquez (1933) observed the association of their fungus with *Gelatinosporium fulvum* Peck and concluded that it was the conidial stage. Cultural studies have shown this to be correct. There is no valid distinction between *Micropera* and *Gelatinosporium* and this is a typical *Micropera*.

- DERMATEA ARIAE (Pers.) Tul. Sel. Fung. Carp. 3: 160. 1865.
Peziza Ariae Pers. Myc. Eur. 1: 325. 1822.
Tympanis Ariae Fries, Syst. Myc. 2: 175. 1822.
Tympanis inconstans Fries, Summa Veg. Scand. 400. 1849.
Cenangium inconstans Fuckel, Symb. Myc. 268. 1869-70.
Cenangium subnitidum Cooke & Phill. Grevillea 3: 186. 1875.
Phaeangella subnitida Massee, Brit. Fung. Fl. 4: 137. 1895.
Sphaeria Cotoneastri β *Sorbi* Fries, Syst. Myc. 2: 494. 1823.
Micropera Sorbi Sacc. Michelia 2: 104. 1880.
Sphaeronema pallidum Peck, Ann. Rep. N. Y. State Mus. 25: 85. 1873.

Apothecia erumpent, gregarious, separate or in small clusters of two to four, circular or undulate, sessile, narrowed below, 0.4-0.8- (1.0) mm. in diameter, 0.2-0.4 mm. in height, dark reddish-brown to black, slightly furfuraceous to glabrous, hard, leathery to horny in consistency, more fleshy-leathery when moist, hymenium concave to plane, black, with a thick, raised, brownish margin; tissue

of the hypothecium compact, pseudoparenchymatous, composed of irregular thick-walled cells, $3-8\ \mu$ in diameter, arranged in more or less vertically parallel rows, curving obliquely toward the outside where the cells are darker and thicker walled, subhymenium a narrow, indefinite zone of slender, interwoven hyphae; asci cylindric-clavate, narrowed into a short stalk, eight spored, $(60)-70-90-(100) \times 8-10\ \mu$; ascospores ellipsoid-fusiform, hyaline to pale yellowish, one to four celled, straight or slightly curved, irregularly biseriate to uniseriate below, $(10)-12-18-(22) \times 3-5\ \mu$; paraphyses hyaline, filiform, septate, simple or branched, $1.5-2.5\ \mu$ in diameter, the tips swollen up to $5\ \mu$ and glued together forming a yellowish epithecium.

Conidial fruiting bodies erumpent, gregarious, usually separate, sometimes two or three together, bluntly conical, about $250-350\ \mu$ in diameter at the base, $250-500\ \mu$ in height, reddish-brown to olivaceous or black, slightly furfuraceous to glabrous, hard, horny in consistency, becoming softer and more fleshy when moist, containing a single, ovoid or slightly chambered cavity; tissue pseudoparenchymatous in the basal stroma, composed of irregular, hyaline cells about $3-6\ \mu$ in diameter, becoming prosenchymatous above, composed of ascending, parallel to more or less interwoven hyphae $2-3\ \mu$ in diameter, brownish at the outside; conidiophores hyaline, cylindric, simple or branched, continuous or septate, pointed at the tip, $20-40 \times 1.5-2.0\ \mu$; conidia hyaline to pale yellowish-green, elongate-fusiform, sickle-shaped, occasionally sigmoid or almost straight, ends pointed, one or two celled, $(12)-15-20-(25) \times 2.0-4.0\ \mu$, microconidia not observed in nature.

Host: *Sorbus* spp.

EXSICCATI: Krieg. Fung. Sax. 1516; Rehm Ascom. 1057; Roum. Fung. Sel. Gall. Exs. 537; Phill. Elv. Brit. 94 (as *Cenangium subnitidum* Cooke & Phill.); Syd. Myc. Germ. 1992 (*Micropera Cotoneastri* (Fries) Sacc.); Fung. Columb. 571.

SPECIMENS EXAMINED: University of Toronto Herbarium. On *Sorbus americana*. 4495 (68), 4496 (69), 7283 (180), 7918 (332), 7921 (406), 7922 (331), Temagami Forest Reserve, Ontario.

Herbarium of J. W. Groves. On *Sorbus americana*. 235, 296, 628 (ex herb. L. O. Overholts 18873), Temagami Forest Reserve, Ont.—609, 626 (ex herb. U. S. D. A. Path. and Myc. Coll. C. L. Shear 4161), Duchesnay, Que.—641 (L. E. Wehmeyer 402), Truro, Nova Scotia. On *Sorbus aucuparia*. 577, Uppsala, Sweden, coll. L. E. Wehmeyer, Aug. 18, 1937.

On malt extract agar the colonies reach a diameter of 5-6 cm. in three weeks. The margin is almost colorless and closely appressed. The aerial mycelium is at first thin, whitish, cottony-fluffy, becoming much more abundant toward the centre of the colony, much tufted, and variously colored from whitish to pale yellow, ochraceous, or "clay color" to "olive ocher" (Ridgway). Conidial fruiting bodies are produced only occasionally as fleshy stromata, usually about the size and shape of those found in nature, but sometimes much larger and almost globose. They are whitish to yellowish or buff, covered with a short, downy mycelium, and usually containing a single, more or less lobed cavity, the larger fruiting bodies splitting open very widely. The tissue is composed of closely interwoven hyphae. Occasionally cultures will be obtained which grow more slowly and produce less aerial mycelium, but these produce the same type of conidial fruiting body and spores; in fact they seem to fruit more readily than the commonly obtained colony with more aerial mycelium. The conidia and conidiophores are typical of those found in nature. Microconidia are hyaline, filiform, usually more or less hooked at one end, one celled, $10-20-(25) \times 1.5-2.0 \mu$.

On twigs of *Sorbus* some whitish to buff aerial mycelium is developed at the point of inoculation and may spread more or less over the twig. Conidial fruiting bodies arise as small, erumpent, fleshy stromata, at first rounded, tomentose, then becoming more or less flask-shaped to conical, blackish and glabrous above, about 0.5 mm. in diameter at the base, and the same in height. They do not sporulate very freely, most of them remaining sterile and developing into large, cottony, mycelial tufts. The tissue structure is similar to that found in nature, the conidia and conidiophores are typical and microconidia have been observed.

This species is characterized chiefly by its occurrence on *Sorbus*, brownish to black, not strongly erumpent apothecia, small asci and ascospores, the type of conidial fruiting body and the short, slender conidia. It has been known for a long time in Europe where it is apparently more common than in North America. The conidial fruiting bodies are usually more abundant, and frequently more conspicuous than the apothecia. The genetic connection of the two stages has long been assumed, but proof based on cultural

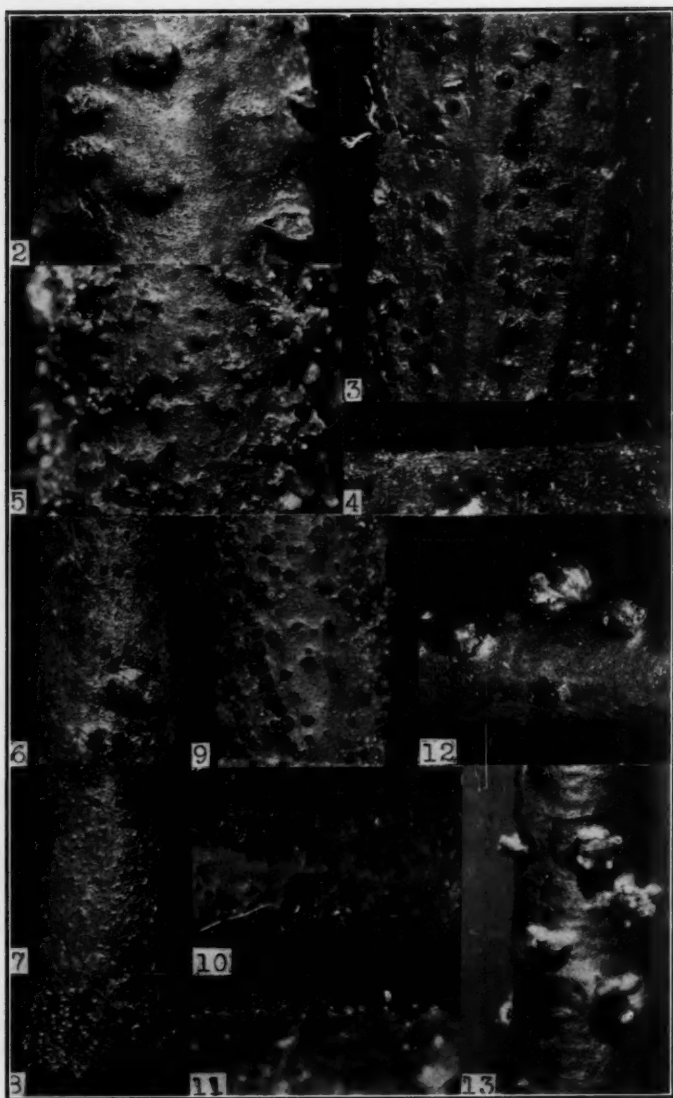


FIG. 2, *Dermatea molliuscula*; 3-5, *D. Viburni*; 6-8, *D. Hamamelidis*; 9-11, *D. Ariae*; 12, 13, *D. molliuscula*.

studies has hitherto been lacking. Von Höhnelt (1916) has given a list of synonyms of the conidial stage.

Cenangium subnitidum Cooke & Phill., which is here included as a synonym, was originally described by Cooke (1874) from a specimen said to be on *Alnus* and distributed in Phill. *Elv. Brit.* 94. Examination of the specimen in the Farlow Herbarium disclosed that it was identical with *Dermatea Ariae*. Both perfect and imperfect stages were present and agreed with the original description of *C. subnitidum*. At the writer's request, the wood of the host was examined by Dr. R. H. Wetmore who stated that it was definitely not *Alnus* but *Sorbus*. Thus there can be no doubt that *C. subnitidum* was based on a misdetermination of the host.

Dermatea Hamamelidis (Peck) comb. nov.

Patellaria Hamamelidis Peck, Ann. Rep. N. Y. State Mus. 33: 32. 1880.

Dermatella Hamamelidis Durand, Bull. Torrey Club 29: 464. 1902.

Dermatella Hamamelidis Ellis & Ev. Proc. Phila. Acad. Sci. 45: 149. 1893.

Lecanidion Hamamelidis Sacc. Syll. Fung. 8: 800. 1889.

Apothecia erumpent, scattered or more or less in rows, separate or in small clusters, circular or somewhat undulate, sessile, narrowed below, 0.3–0.8 mm. in diameter, 0.2–0.4 mm. in height, dark reddish-brown to black, hard, leathery to horny in consistency, becoming more fleshy-leathery when moist, hymenium concave to plane or finally convex, slightly roughened, margin at first raised, later almost disappearing; tissue of the hypothecium compact, pseudoparenchymatous, composed of more or less elongated to almost isodiametric cells 5–12 μ in diameter, fairly thick walled, dark brown to almost hyaline, arranged in more or less vertically parallel rows, curving obliquely toward the outside where the cells are smaller, darker, and thicker walled; subhymenium a narrow zone of filamentous, interwoven hyphae; asci cylindric-clavate, short stalked, eight spored, (70)–80–100–(120) \times (10)–12–15 μ ; ascospores ellipsoid-fusiform, hyaline to yellowish, straight or slightly curved, irregularly biseriolate, one to four celled, (13)–15–20–(22) \times 5.0–7.5 μ ; paraphyses hyaline, filiform, septate, simple or branched, 1.5–2.0 μ in diameter, the tips slightly swollen and glued together forming a yellowish epithecium.

Conidial fruiting bodies minute, about 150–200 μ in diameter,

developing beneath the outer bark layers and splitting them, appearing as small, thickly scattered, blister-like elevations in the bark with gray spore masses emerging through them when moist. In section they appear as an acervulus-like structure with a thin basal layer about $5-8\ \mu$ in thickness, composed of hyaline, indistinct, slender, interwoven hyphae which curve upwards to form the hyaline, cylindric, simple conidiophores, $10-25 \times 2.0\ \mu$, tapering to a slender tip; conidia elongate-fusiform to sub-filiform, hyaline, one or two celled, straight or curved, sometimes one end narrower and more curved than the other, $(15)-18-25-(32) \times 4.5-6.0\ \mu$. No microconidia have been observed.

Host: *Hamamelis virginiana* L.

EXSICCATI: Ellis N. Am. Fungi 2634; Fung. Columb. 2016.

SPECIMENS EXAMINED: University of Toronto Herbarium. On *Hamamelis virginiana*. 4374 (57), 7402 (162), 6565 (271), 7928, Toronto, Ont.—unnumbered (285), Pixley's Falls, N. Y. Coll. R. F. Cain.

Herbarium of J. W. Groves. On *H. virginiana*. 661 (ex herb. L. O. Overholts 21692), Stoyestown, Pa.—667 (ex herb. L. O. Overholts 20139), English Center, Lycoming Co., Pa.

Durand Herbarium. 6096, N. Greenbush, N. Y. Part of the type. 1048, Lyndonville, N. Y. Coll. C. E. Fairman (as *Dermatella Hamamelidis* Ell. & Ev.).

On malt extract agar the fungus grows very slowly reaching a diameter of 2–2.5 cm. in five weeks, forming heaped up colonies of firm consistency with a more or less wavy margin. The surface is often deeply radially furrowed, sometimes even, very variable in color, whitish to buff, yellowish-green, brown, or almost black. The conidial fruiting bodies are small, almost globose stromata, $300-400\ \mu$ in diameter, composed of closely interwoven, hyaline hyphae about $3-5\ \mu$ in diameter, and containing a more or less lobed cavity. The walls surrounding the cavity are about $25-50\ \mu$ in thickness and they tear open widely at the top. The conidia are typical but the conidiophores are sometimes longer than in nature.

On twigs of *Hamamelis* very little aerial mycelium is produced, but sometimes a little whitish to buff or brown, closely appressed aerial mycelium develops around the point of inoculation. The conidial fruiting bodies are small, erumpent, rounded stromata, whitish to buff, about $250-400\ \mu$ in diameter, covered with a short,

aerial mycelium. The microscopic structure is similar to those formed on agar. No microconidia have been observed.

This species is characterized by its occurrence on *Hamamelis*, small, blackish, not strongly erumpent apothecia, relatively short and broad conidia, and the type of conidial fruiting body. As far as known the conidial stage is undescribed but it may be regarded as a reduced *Micropera*.

This fungus was first described by Peck (1880) as *Patellaria Hamamelidis* and transferred to *Dermatella* by Durand (1902). In the meantime Ellis and Everhart (1893) had described it independently as a new species of *Dermatella*. The genus *Dermatella* was erected by Karsten (1871) and separated from *Dermatea* by having septate ascospores. Since it is possible to find septate ascospores in all *Dermatea* species including *D. Cerasi* (Pers.) Fries, the type of the genus, this cannot be regarded as a valid generic distinction. *Dermatella* must, therefore, be regarded as a synonym of *Dermatea* and it is necessary to transfer this species to *Dermatea*.

***Dermatea Viburni* sp. nov.**

Sphaeronema hystricinum Ellis, Bull. Torrey Club 6: 106. 1876.

Sphaerographium hystricinum Sacc. Syll. Fung. 3: 597. 1884.

Chondropodium hystricinum Höhnelt, Frag. Myk. 958. 1916.

Sphaerographium hystricinum var. *Viburni* Dearn. & House, Bull. N. Y. State Mus. 197: 35. 1917.

Apotheciis erumpentibus, sparsis, solitariis vel 2-6 congregatis, sessilibus, versus basin leviter attenuatis, orbicularibus vel undulatis, parvis, 0.3-0.6 mm. diam., 0.2-0.5 mm. altis, atris, duris, coriaceis vel corneis, in humido carnosocoriaceis; hymenio atro, primitus concavo dein plano vel convexo, margine initio elevato dein evanescente; hypothecio prosenchymato; ascis cylindracco-clavatis, breviter stipitatis, octosporis, (50)-60-75 \times 8-12.5 μ ; ascosporis ellipsoideo-fusiformibus, hyalinis vel leviter fuscis, rectis vel leviter curvatis, continuis vel uniseptatis, irregulariter biseriatis vel subuniseriatis, (10)-14-18-(20) \times 3.5-5.5 μ ; paraphysibus hyalinis, filiformibus, septatis, ramosis, 1.5-2.0 μ diam., apice ad 3 μ leviter incrassatis, epithecium formantibus.

Apothecia erumpent, separate or in small clusters of 2-6, sessile, slightly narrowed below, circular or slightly undulate, 0.3-0.6-(1.0) mm. in diameter and 0.2-0.5 mm. in height, dark brown to black, hard, leathery to horny in consistency, becoming more fleshy-leathery when moist; hymenium black, at first concave, becoming plane to convex, margin at first raised, later almost disappearing;

hypothecium composed of closely interwoven, hyaline to pale brownish, thick-walled hyphae about $5-8\mu$ in diameter, in the upper part more or less vertically parallel, curving obliquely toward the outside where the walls are darker colored; subhymenium a narrow, brownish zone; asci cylindric-clavate, short stalked, eight spored, $(50)-60-75 \times 8-12.5\mu$; ascospores ellipsoid-fusiform, hyaline becoming slightly yellowish, straight or slightly curved, one or two celled, $(10)-14-18-(20) \times 3.5-5.5\mu$; paraphyses hyaline, filiform, septate, much branched, $1.5-2.0\mu$ in diameter, the tips slightly swollen up to 3μ and glued together forming a yellowish epithecium.

Conidial fruiting bodies erumpent, thickly scattered or more or less in rows, single or with two or three arising from the same basal stroma, cylindric-subulate, dark brown to black, often with a reddish tinge, especially when moist, base about $0.3-0.5$ mm. in diameter and the beaks about 1 mm. long, hard, leathery to horny, becoming more fleshy when moist; tissue of the basal stroma composed of closely interwoven, ascending, hyaline, thick-walled hyphae about $5-8\mu$ in diameter, becoming darker colored and thicker walled at the outside, tissue of the beak similar in structure, the basal stroma containing a single, ovoid to elongated cavity about $150-250\mu$ in diameter; conidiophores cylindric, septate, occasionally branched, tapering to a slender point, $15-30 \times 2.0-2.5\mu$, lining the cavity and the beak; conidia elongated to sub-filiform, hyaline, sickle-shaped or sigmoid to almost straight, usually with one end more attenuated than the other, one celled, $(25)-30-45 \times 2.5-4.0\mu$. No microconidia have been observed in nature.

Host: *Viburnum* species.

Type: University of Toronto Herbarium 7937, Hatchley, Ontario.

EXSICCATI: Ellis, N. Am. Fungi 337 (*Sphaerographium hystri-cinum*); Rel. Farl. 198a, 198b (*S. hystricinum*).

SPECIMENS EXAMINED: University of Toronto Herbarium. On *Viburnum Lentago* L. 7937 (433), Hatchley, Ont. On *V. cassinoides* L. 4460, 4461, 6976 (230), 8432, Temagami Forest Reserve, Ont.—4558, Wilcox Lake, Ont.—7171, 7266 (275), north of Parry Sound, Ont.—unnumbered, 7th Lake, Inlet, N. Y. On *V. nudum* L. ex Farlow Herbarium, Abbey Rd., Ripton, Vt. Coll. E. A. Burt, Mar. 6, 1897.

Herbarium of J. W. Groves. On *V. cassinoides* L. 268, Temagami Forest Reserve, Ont.—600, Duchesnay, Que.

On malt extract agar the cultures grow slowly, reaching a diameter of 2.5–3.0 cm. in three weeks. The colonies are very irregular with a lacerate margin, whitish at first, then brownish or buff to avellaneous. The aerial mycelium is usually short, downy to velvety, sometimes almost absent, occasionally forming whitish, cottony tufts. Conidial fructifications are similar in both ascospore and conidial cultures. In color and consistency they are similar to those found in nature, but they do not develop the characteristic beaks. They are very irregular in shape and unevenly rounded, up to 3 mm. in diameter and 1 mm. in height, glabrous, with one or more irregular openings through which the conidia emerge in grayish-white masses. The tissue of the stroma is composed of hyaline or slightly colored, closely interwoven hyphae about $3\text{--}5\ \mu$ in diameter. A striking feature is the presence of a deep red pigment irregularly distributed throughout the stroma but especially in the upper part surrounding the pycnidial cavities. These cavities are irregular in shape and more or less lobed, finally opening very widely. The conidia are typical of those found in nature, the conidiophores sometimes longer. Microconidia hyaline, filiform, mostly curved, one celled, $8\text{--}15 \times 1.5\text{--}2.0\ \mu$.

On twigs of *Viburnum* very little aerial mycelium is produced. Conidial fructifications which exhibit considerable variation in the form of the stroma are developed, and none have been observed quite typical of the form as it occurs in nature. The fruiting bodies are erumpent, rounded or irregular in shape, about 0.5–1.0 mm. in diameter, reddish-brown to black, glabrous or covered with a short, brown, aerial mycelium. Many do not elongate but split open irregularly, while others become more or less elongated, up to 2 mm. in height. They are thicker than in nature and may open at the top or remain sterile. Sometimes a cluster of short beaks will arise from one basal stroma which may be up to 2 mm. in diameter. The stroma frequently continues to develop vegetatively, eventually forming erect, brown, cottony tufts scattered over the twigs and never sporulating. The tissue structure is similar to that found in nature but the hyphae are sometimes thinner walled and more loosely interwoven, especially toward the outside. The cavities are more irregular in shape and frequently more or less

lobed. The conidia and conidiophores are typical but the latter may be longer than in nature.

This fungus is common on *Viburnum* in the Temagami Forest Reserve but usually only the conidial stage is found. The apothecia were only discovered after much search for a perfect stage and are usually very scarce and much less conspicuous than the conidial fruiting bodies. Apothecia of *Tympanis fasciculata* Schw. are frequently found on the same twigs and are somewhat similar in gross appearance, but can readily be distinguished by the many-spored asci and have a *Pleurophomella* species as the conidial stage. *Dermatea minuta* Peck is a *Pezicula* and has a *Cryptosporiopsis* species as the conidial stage. *Dermatea viburnicola* Ellis is an *Encoelia*, and has only produced a microconidial stage in culture. No fungus described on *Viburnum* appeared to agree with this species which is accordingly described as new.

Sphaerographium hystricinum was originally described by Ellis (1876) and said to be on *Viburnum*. The description by Saccardo (1884), however, gives the host as *Azalea viscosa*. Peck (1885) reported it on *Viburnum nudum* and his figures unquestionably illustrate the fungus studied here. Dearness and House (1917) apparently following Saccardo and regarding the *Azalea* form as the type, re-described the *Viburnum* form as a new variety. It is possible that this, or a similar species, may occur on *Azalea*, but I have seen no material on this host and cultural studies would be necessary before a final decision as to its identity could be reached. Von Höhnelt (1916) suggested that *S. hystricinum* would prove to be the conidial stage of a *Godronia*, but the cultural studies have demonstrated that it belongs to a *Dermatea*.

The four species of *Dermatea* described above were chosen for the purpose of illustrating some of the range of variation in the form of the conidial stroma in this genus. The range of variation in the form of the conidial stroma of species of the related genus *Pezicula* was described by the writer (1939), and it was noted that on the basis of the form of the conidial stroma, these imperfect stages of the same discomycetous genus could be referred to widely separated families of the Fungi Imperfecti. In *Dermatea* a somewhat similar range of variation in the form of the conidial stroma

is found, but the conidia, themselves, are elongated to sub-filiform, while in *Pezicula* they are oblong-ellipsoid to ovoid.

The conidial stage of *Dermatea molliuscula* illustrates a typical *Micropera*. It is very similar in form to *Micropera Drupacearum* Lév., the conidial stage of *Dermatea Cerasi* (Pers.) Fries, and the type of the genus *Micropera*. In comparing this with a typical *Cryptosporiopsis* as illustrated by the conidial stages of species such as *Pezicula acericola* (Peck) Sacc. (Groves 1938), *P. Hamamelidis* Groves & Seaver (Groves 1939), *P. Alni* Rehm, or *P. aurantiaca* Rehm (Groves 1940), we find that both consist essentially of a stroma containing one or more cavities, although in *Micropera* the stroma is usually more erumpent and the cavities deeper and more flask-shaped. The similarity in the range of variation in the two genera can be illustrated if we compare the conidial stages of *Dermatea Hamamelidis* and *Pezicula Rubi*, *D. Ariae* and *P. Corni*, and *D. Viburni* and *P. pruinosa*. As in *Cryptosporiopsis*, so also in *Micropera*, the conidial fruiting bodies in culture tend to approach a common form consisting of a more or less globose stroma containing one or more cavities, but the conidia remain typical of those found in nature.

The genera *Dermatea* and *Pezicula* are separated chiefly on the basis of the color and consistency of the apothecia, although other differences exist such as the presence, in *Dermatea*, of a more definite epithecium and, as a rule, proportionately narrower asci and ascospores. In the conidial stages a correlation exists between these characters and the form of the conidial spore, but does not exist between them and the form of the conidial stroma. On the contrary a parallel series of variations in the form of the conidial stroma is found in both *Dermatea* and *Pezicula*. It is concluded, therefore, that the form of the conidial spore is a more stable character, and thus of greater taxonomic value than the form of the conidial stroma.

Although in the majority of species of *Dermatea* and *Pezicula* this correlation certainly exists, it does not hold for every species. The writer has previously pointed out two exceptions, *Dermatea acerina* (Peck) Rehm (Groves 1938) with apothecia like a *Dermatea* but conidia like a *Cryptosporiopsis*, and *Pezicula alnicola* Groves (Groves 1940) with apothecia like a *Pezicula* but conidia

like a *Micropera*. The question of the true relationships of these species cannot be satisfactorily answered at this time, but the writer is of the opinion that, in the present state of our knowledge of this group, it is preferable to leave these aberrant species for the time being in the genus to which they would be assigned on the basis of the characters of the perfect stage.

ACKNOWLEDGMENTS

The writer is indebted to Professor H. S. Jackson, Department of Botany, University of Toronto, for his continued interest and constructive suggestions; and to Dr. D. H. Linder and Dr. R. H. Wetmore, Harvard University, for their assistance in the determination of the host of the type specimen of *Cenangium subnitidum*.

CENTRAL EXPERIMENTAL FARM,
OTTAWA, CANADA

LITERATURE CITED

- Cash, Edith K. *Cenangium molliusculum*. *Mycologia* 29: 303-304. 1937.
- Cooke, M. C. British fungi. *Grevillea* 3: 177-186. 1875.
- Dearness, J. & House, H. D. *Bull. N. Y. State Mus.* 197: 1-122. 1917.
- Durand, E. J. Studies in North American Discomycetes. II. Some new or noteworthy species from central and western New York. *Bull. Torrey Club* 29: 458-465. 1902.
- Ellis, J. B. South Jersey fungi. *Bull. Torrey Club* 6: 106-109. 1876.
- & Everhart, B. M. New species of North American Fungi from various localities. *Proc. Acad. Nat. Sci. Phil.* 45: 128-172. 1893.
- Groves, J. Walton. *Dermatea acerina* and *Pezicula acericola*. *Mycologia* 30: 416-430. 1938.
- . Some *Pezicula* species and their conidial stages. *Can. Jour. Res. C* 17: 125-143. 1939.
- . Three *Pezicula* species occurring on *Alnus*. *Mycologia* 32: 112-123. 1940.
- Höhnelt, F. von. Fragmente zur Mykologie. *Sitz-ber. Akad. Wien* 125: 1-112. 1916.
- Karsten, P. A. *Mycologia fennica. Pars prima. Discomycetes.* *Bidr. Kännedom af Finlands Natur och Folk. Helsingfors.* 19th part. p. 1-263. 1871.
- Nannfeldt, J. A. Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten. *Nova Acta Soc. Sci. Upsal.* IV. 8: 1-368. 1932.
- Peck, C. H. *Ann. Rep. N. Y. State Mus.* 33: 11-49. 1880.
- . *Ann. Rep. N. Y. State Mus.* 38: 77-138. 1885.

- Rehm, H. Ascomyceten: Hysteriaceen und Discomyceten. Rab. Krypt. Fl. von Deutschland, Österreich und der Schweiz. 2 Aufl. Abt. III. Nachträge p. 1209-1270. 1896.
- . Zur Kenntniss der Discomyceten Deutschlands, Deutsch-Österreichs und der Schweiz. Ber. Bayer. Bot. Ges. 13: 102-206. 1912.
- Saccardo, P. A. Sylloge fungorum 3: 1-860. 1884.
- Schweinitz, L. v. Synopsis fungorum in America borealis media degentium. Trans. Am. Phil. Soc. II. 4: 141-316. 1832.
- Seaver, F. J. & Velasquez, J. *Dermata* and *Pezicula*. Mycologia 25: 139-149. 1933.
- Tulasne, L. R. & C. Selecta fungorum carpologia (Transl. by Grove) 3. Paris. 1865.

EXPLANATION OF FIGURES

FIG. 1. *Dermatea molliuscula*, A, asci, ascospores, and paraphyses, B, conidiophores and conidia; *D. Ariae*, C, asci, ascospores, and paraphyses, D, conidiophores, conidia, and microconidia; *D. Hamamelidis*, E, asci, ascospores, and paraphyses, F, conidiophores and conidia; *D. Viburni*, G, asci, ascospores, and paraphyses, H, conidiophores, conidia, and microconidia.

FIGS. 2-13. 2, apothecia of *Dermatea molliuscula*; 3, apothecia of *D. Viburni*; 4, conidial stage of *D. Viburni* in nature; 5, conidial stage of *D. Viburni* on a twig of *Viburnum* in culture; 6, apothecia of *D. Hamamelidis*; 7, conidial stage of *D. Hamamelidis* in nature; 8, conidial stage of *D. Hamamelidis* on a twig of *Hamamelis* in culture; 9, apothecia of *D. Ariae*; 10, conidial stage of *D. Ariae* in nature; 11, conidial stage of *D. Ariae* on a twig of *Sorbus* in culture; 12, conidial stage of *D. molliuscula* in nature; 13, conidial stage of *D. molliuscula* on a twig of *Betula* in culture. All $\times 4$ approx.

A NEW HOST FOR TAPHRINA BACTERIOSPERMA

W. WINFIELD RAY¹

(WITH 2 FIGURES)

Taphrina bacteriosperma Johans. was first described by Johanson (1) in 1887. He found the fungus on the leaves and stems of *Betula nana* L. in the Jemtland province of Sweden. In addition, he reported the fungus had also been collected in Greenland. Mrs. Patterson (2) called a fungus collected on *Betula glandulosa* Michx. from Mt. Washington, New Hampshire, *T. bacteriosperma*. Seymour (3) lists this species as occurring on *B. occidentalis* Hook, *B. nana*, and *B. glandulosa*. None of the collections on which this information was based was examined by the writer.

A collection of leaves of *Betula lutea* Michx., which were affected by *T. bacteriosperma*, was forwarded for study by H. S. Jackson. As far as could be ascertained, this collection represented the first time this species of *Taphrina* had been found on *B. lutea* anywhere in the world. An unnamed species of *Taphrina* has been reported affecting this host in the Plant Disease Reporter² on several occasions. The fungus in question may have been *T. bacteriosperma*.

Usually the mycelium of *T. bacteriosperma* is confined to the region of the leaf between the cuticular and epidermal layers on the lower surface, although it also may occur in a similar position on the upper side. No vegetative mycelium inhabits the inner tissues of the leaf, but, even so, the inner cells of the host are stimulated to such an extent that a hypertrophic condition results.

Infection results in definite, localized, blister-like lesions, or the entire leaf may be affected (FIG. 1). Diseased areas are concave below and convex above, and the thickness of a lesion is 250–300 μ , whereas, the thickness of a healthy leaf seldom exceeds 125 μ . The color of the diseased areas is yellow to yellowish-red.

¹ To Dr. H. S. Jackson for his generosity in providing the material upon which this paper is based grateful acknowledgment is hereby made.

² Suppl. 96: 242. 1936; 21: 34. 1939.

The asci (FIG. 2B) arise from the subcuticular mycelium and are crowded together in a compact layer. The majority of the asci are wider below than at the top, although they may be nearly cylindrical



FIG. 1. Blister-like lesions caused by *Taphrina bacteriosperma* on the leaf of *Betula lutea*, nat. size.

in some cases. Both the apical and basal ends are rounded to slightly truncate. No basal cell exists in this species.

Johanson gave the size of the asci as $47-80\ \mu$ long \times $14-20\ \mu$ wide, but the writer found, as did Mrs. Patterson, that they were somewhat smaller. The asci from the collection made by Jackson were $38-65\ \mu$ long \times $14-17\ \mu$ wide. The base of the ascus occasionally attained a width of $25\ \mu$. Many small ellipsoidal spores, $3-7\ \mu$ long \times $1-2\ \mu$ wide, filled the asci.

A species with which *T. bacteriosperma* might be confused is *T. carnea* Johanson. This latter fungus produces large, thickened, red, gall-like lesions on the upper surface of the leaves of various species of *Betula*. Its asci (FIG. 2A) are similar to those of *T.*

bacteriosperma in the presence of many spores in each ascus and the absence of a basal cell. However, the asci of *T. carnea* are longer and the bases less expanded than those of *T. bacteriosperma*.

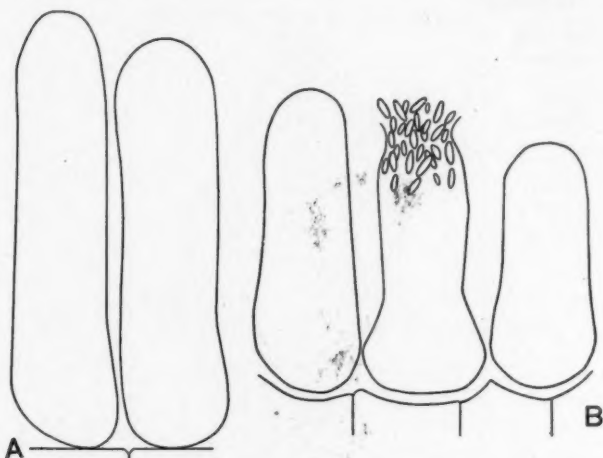


FIG. 2. A, asci of *Taphrina carnea* from leaf of *Betula pubescens*; B, asci and spores of *Taphrina bacteriosperma* from leaf of *Betula lutea*. Drawings $\times 893$.

They are $58-80\ \mu$ long $\times 12-17\ \mu$ wide in the specimens studied by the writer.

Taphrina carnea is common in Europe, and it has been reported from North America on *Betula glandulosa* and *B. nana* by Seymour (3).

SPECIMENS EXAMINED

Taphrina bacteriosperma on *Betula lutea*.

Canada; Lake Temagami, Ontario, Collected by H. S. Jackson.

In the University of Toronto Cryptogamic Herbarium, No. 1045.

Taphrina carnea on *Betula pubescens*.

Norway: Kongsvell, Collected by H. H. Whetzel. In the herbarium of the Department of Plant Pathology, Cornell University, No. 23602.

SUMMARY

Taphrina bacteriosperma occurring on the leaves of *Betula lutea* in Canada is recorded on that host for the first time.

The outstanding differences in the symptoms caused by this species and *T. carnea*, and the morphological similarities and differences between the two fungi, have been discussed.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY,
AGRICULTURAL AND MECHANICAL COLLEGE,
STILLWATER, OKLAHOMA

LITERATURE CITED

1. Johanson, C. J. Studier ofer svampslagtet *Taphrina*. Bihang Svensk. Vet. Akad. Handlingar 13: 3-28. 1887.
2. Patterson, F. W. A study of the North American parasitic Exoasceae. Bull. Lab. Nat. Hist. Univ. Iowa 3: 89-135. 1895.
3. Seymour, A. B. Host index of the fungi of North America. p. 1-732. 1929.

TWO NEW GENERA OF DISCOMYCETES FROM THE OLYMPIC NA- TIONAL FOREST¹

BESSIE B. KANOUSE AND ALEXANDER H. SMITH

(WITH 1 FIGURE)

The spring season of 1939 was spent by the junior author in the Olympic National Forest, Washington, on a mycological expedition. Among the numerous collections of Discomycetes that were made during that time are two that are here described as new. For them two new genera are erected in the family Pezizaceae. These fungi were found growing at an altitude of 5000 feet in the Hudsonian Life Zone in small areas uncovered by recently melted snow.

Gelatinodiscus gen. nov.

Apothecia gelatinosa, mollia; stipes glaber, gelatinosus, brevis; asci cylindracei, J +; sporae ellipsoideae, leves, subflavae; paraphyses filiformes, ramosae. Species typica, *G. flavidus* sp. nov.

Gelatinodiscus flavidus sp. nov. (FIG. A-F)

Apothecia concava subexplanata vel convexa, gelatinosa, mollia, flava, 2-5 mm. lata; stipes 2-4 mm. altus, 1 mm. crassus, flavus, levis, gelatinosus; asci cylindracei, 150-160 \times 15-17 μ , octospori, J +; sporae ellipsoideae, 2-guttulatae, 26-34 \times 9-11 μ , subflavae; paraphyses filiformes, racemosae et curvatae. Specimen typicum legit prope Sol Duc Park, Olympic National Forest, Washington, June 20, 1939, A. H. Smith n. 14488, in Herb. Univ. of Mich. conservatum.

Apothecia solitary, stipitate, gelatinosus when fresh, drying fragile, reaching a diameter of 5 mm. opening cup-shaped, becoming convex, "yellow ochre" (R)² throughout, drying "dark olive," shrinking greatly on drying, hypothecium pseudoparenchymatous, exciple consisting of small thin-walled cells interspersed with groups

¹ Papers from the Herbarium of the University of Michigan.

² The colors cited in quotation marks are those of R. Ridgway, Color Standards and Color Nomenclature. 1912.

of small thick-walled cells which extend downwards into the stipe; stipe slender, measuring 2-5 mm. high and 1 mm. thick, broadly attached to the substratum; asci cylindric, thin-walled, operculate, apices turned blue with iodine, 8-spored, $150-160 \times 15-17 \mu$; spores oblong-ellipsoid, irregularly biseriate in the ascus, contain-

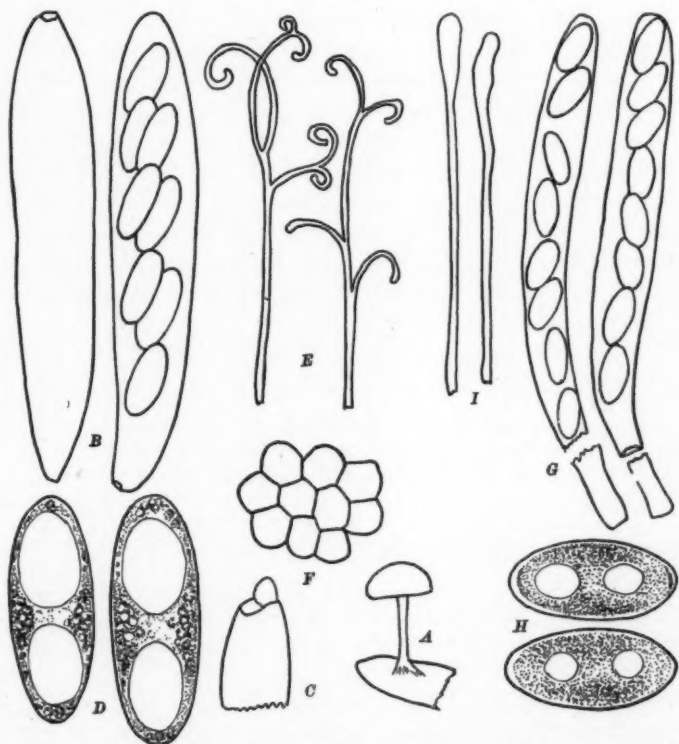


FIG. 1. A-F, *Gelatinodiscus flavidus*. A, sketch of mature ascophore showing convex surface of apothecium; B, mature asci $\times 350$; C, sketch showing operculum; D, spores $\times 1100$; E, paraphyses showing type of branching; F, sketch of hypothecial cells. G-I, *Pseudocollema cartilagineum*. G, upper portion of mature asci; H, spores $\times 1100$; I, paraphyses.

ing two large oil drops, smooth, greenish-yellow, $26-34 \times 9-11 \mu$; paraphyses hyaline, slender, branched irregularly, curved and slightly enlarged at the tips, 1.5μ thick.

On *Chamaecyparis nootkatensis* Sudw. lying in seepage from a

snowbank, 5000 ft. elevation, Sol Duc Park, Olympic National Forest, Washington, June 20, 1939. A. H. Smith n. 14488. Type deposited in the Herbarium of the University of Michigan.

The genus *Gelatinodiscus* belongs in the Pezizaceae. It is placed near *Pseudombrophila* although no close relationship is claimed. The operculate asci, large *Peziza*-like spores and the friable consistency of the dry apothecia are characters that are like those of other species placed in that family. In the fresh condition the gelatinous nature superficially allies it with the Bulgariaceae, particularly with the genus *Ombrophila*, but instead of drying horny as do species in that genus, or in other genera in the Bulgariaceae, *Gelatinodiscus flavidus* dries very fragile. On account of this characteristic it is somewhat difficult to make a microscopic mount that holds together sufficiently well for a satisfactory study. A bright yellow color exudes from the hypothecium and stains the mounting medium.

***Pseudocollema* gen nov.**

Apothecia coprophila, gregaria, sessilia, enascentia e cartilaginosa stromatica basi, subturbinata, mollia, catinosa; asci anguste cylindracei, J +; spores ellipsoideae, nonseptatae; paraphyses filiformes. Species typica, *P. cartilagineum*.

***Pseudocollema cartilagineum* sp. nov. (FIG. G-I)**

Apothecia gregaria, sessilia, enascentia e cartilaginosa stromatica basi, mollia, carinosa, aurantiaca, 1 mm. alta, 1 mm. lata; asci anguste cylindrici, 230-250 \times 15-17 μ , octospori, J —; spores leves, hyalinae, nonseptatae, 19-21 \times 9-10 μ ; paraphyses filiformes.

Apothecia sessile, thickly gregarious, produced upon a thick cartilaginous stroma-like base formed over a dung heap, at first globose, becoming subturbinate, 1 mm. wide, 1 mm. high, soft, fleshy, bright orange throughout, fading when dry to brownish, hypothecium pseudoparenchymatous; asci cylindric, collapsing below, 230-250 \times 15-17 μ , 8-spored; spores smooth, hyaline, ellipsoid, 19-21 \times 9-10 μ , parallel or diagonally arranged; uniseriate; paraphyses slender, slightly enlarged above. Iodine does not color the asci.

On a heap of mouse dung, Deer Lake, Olympic National Forest, Washington, 5000 feet elevation, July 10, 1939. A. H. Smith n.

14992. Type deposited in the Herbarium of the University of Michigan.

The apothecia were closely gregarious upon the upper surface of a bulky, irregular, somewhat cartilaginous stromatic mass which measured 9-15 cm. long by 6-10 cm. wide and 10 cm. high. The entire mass nearly covered a heap of mouse dung that was located at the edge of a pool of ice water a short distance from a melting snowbank. The most conspicuous features of the fungus were the brilliant orange color of the apothecia and the curious stromatic mass upon which they were produced. The surface of the stroma, if that term can be applied to this structure, was uneven and wrinkled when fresh. It held its moisture content very tenaciously. Three days of continuous drying over a gasoline stove left it still somewhat rubbery. Eventually it dried down to a thin layer which does not regain its original size of color when moistened. The morphological characters of the apothecia resemble those found in species of *Ascophanus*. The hymenial elements are indeed so similar that without the truly remarkable stroma the fungus would be placed in that genus.

UNIVERSITY OF MICHIGAN,
ANN ARBOR, MICHIGAN

STUDIES IN CERATOSTOMELLA MONTIUM

MARY TAYLOR-VINJE

(WITH 30 FIGURES)

INTRODUCTION

For many years the genus *Ceratostomella* has been an interesting subject for investigation because of the presence, in some of its species, of the phenomenon of deliquescence of asci. Investigations of this phenomenon have brought to light several interesting observations as to the method of development in such "deliquescent type" species. The publication of two reports on the species *C. fimbriata*, one of which describes a new and unique process of ascus multiplication (2) and the other (7) typical ascomycetous development, makes it evident that further work on the "deliquescent type" species of *Ceratostomella* is desirable. The present paper reports an investigation of ascus development in a new species of *Ceratostomella* of the "deliquescent type".

HISTORICAL SURVEY

Because the asci are deliquescent in some of the *Ceratostomellae* they remained undiscovered for quite some time and led many of the early workers (4, 8, 9) to regard the fruiting body as a pycnidium; hence for many years these fungi were considered to be Fungi Imperfecti.

The first correction of this misinterpretation came when Elliott (5), finding that the fruiting body of the fungus *Sphaeronema fimbriata* contained eight spored asci, transferred the species to the genus *Ceratostomella*. He later described (6) the fungus as having a development similar to that found by Harper in *S. Castagnei* except that no croziers were found to initiate ascus formation in *C. fimbriata*.

Sartoris (12) corrected another taxonomic error when he showed that *Sphaeronema adiposum* was, like *C. fimbriata*, an ascomycete belonging to that same genus; he renamed the fungus *Ceratosto-*

mella adiposa. His description of the development in the fungus is especially interesting because it reports a complete absence of sex organs or cell fusions as well as the formation of asci without the intervention of croziers.

Varitchak (13) in a study of *C. Piccae* was the first to report the presence of croziers in a "deliquescent type" species of *Ceratostomella* though he called attention to the fact that such structures are figured though not reported in the work of Elliott (6).

Reports of both the presence and absence of croziers brought renewed interest in the genus, especially in the species *C. fimbriata* upon which most of the subsequent work was done.

Mittmann (10) confirmed Elliott as to the absence of croziers in ascus formation in *C. fimbriata* and further reported that all nuclear divisions in the ascus are confined to a central zone and that the ascus lacks a wall until maturation of the spores.

Andrus and Harter (2) confirmed Mittmann as to the absence of croziers and as to the unwallled condition of the asci in *C. fimbriata*. They further reported that the first nuclear division is characterized by the development of a distinct ascus vesicle which, they suggest, seems to be the membrane of the fusion nucleus. They consider that all three nuclear divisions, as well as delimitation of the ascospores, occur within this vesicle. Andrus and Harter further maintain that this vesicle expands during nuclear division and, by the time the spores are formed, becomes the wall of the ascus. Andrus and Harter are the first workers to report the wall of a fusion nucleus becoming the wall of an ascus, and they suggest that "The procedure is doubtless peculiar to those species of Pyrenomycetes whose asci in their younger stages are without a definite wall."¹

A study by Andrus (1) of *C. multiannulata* reported a development very similar to that found in *C. fimbriata* (2) except that there was never any indication of an ascus vesicle or an endogenous ascus wall although it was noted that spore formation was restricted to the central region of the ascus.

At a later date, in a more intensive study of the ascus development in *C. fimbriata* and *C. moniliformis*, Andrus and Harter (3)

¹ Andrus and Harter: Morphology of reproduction in *Ceratostomella fimbriata*. Jour. Agr. Res. 4: 1059-1098. 1933.

confirmed and extended their earlier views. They came to the conclusion that, in the initiation of asci, not only direct and indirect types of cleavage but also the typical crozier type of cleavage may take part. In both species they found the fusion nucleus to consist of a chromatin network with a nucleolus. In the first division in the ascus of *C. moniliformis* two bilobed (or perhaps four distinct) chromatin bodies were observed on the spindle; in *C. fimbriata* two comma shaped and two bilobed chromatin bodies were found. No reduction division occurred in the ascus according to these authors. No endogenous ascus wall, such as had been previously reported for *C. fimbriata* (2), was found in *C. moniliformis* although a cleavage in the cytoplasm, corresponding in position to the margin of the nuclear vesicle of *C. fimbriata*, was observed. Ascospore formation was observed to occur in a most peculiar manner there being apparently no evidence of astral radiations or free cell formation.

Gwynne-Vaughan and Broadhead (7), in a study of the oft investigated *C. fimbriata*, contrary to the findings of Andrus and Harter (2), observed a typical ascomycetous development. They failed to confirm the absence of ascogenous and ascus walls as reported by Andrus and Harter (2) and could find no evidence of the ascus vesicle figured by Andrus and Harter (2) and Mittmann (10) in the ascus. Asci were observed to develop by typical crozier formation and three was observed to be the haploid chromosome and the gemini number.

From the above discussion it is evident that there exists at present much controversy as to the type of development found in those species of *Ceratostomella* which have deliquescent asci. While it is entirely conceivable that different species within the same genus may have different types of development it is hardly probable that an individual species would show such variance in its development as would be indicated by the reports made for *C. fimbriata* (2, 3, 6, 7, 10). Such controversy over one species makes it evident that an investigation of a new species of *Ceratostomella* may well be of interest.

MATERIALS AND METHODS

Ceratostomella montium Rumbold was used in this investigation. The fungus had been isolated by Dr. Caroline Rumbold² from beetle galleries occurring in lodgepole pine (*Pinus contorta* Loudon). The trees were obtained from a forest on Elk Mountain, Carbon County, Wyoming. The fungus causes a blue stain in the trees and is associated with *Dendroctonus ponderosae* Hopkins and *D. monticolae* Hopkins. The fungus was named and described by Rumbold (11).

The fungus was cultured in petri dishes on a medium consisting of a 4.15 per cent corn meal decoction and 1.5 per cent agar. On this medium mycelial growth was fairly scant and the perithecia readily visible. A constant temperature of 21° C. was used.

Several fixatives were tried but Flemming strong diluted one half with distilled water and Bouin's (Allen's modification) proved to be most satisfactory. The fixative employed was poured directly into the petri dish containing the culture as soon after its removal from the incubator as was possible.

Fixations were made twice a day from the third to the twelfth day of growth, when the perithecial necks were just beginning to elongate, at which time fixations were made every hour for a twenty-four hour period and then daily again until the perithecia were mature.

Following fixation, washing, and dehydration, butyl alcohol was used as the paraffin solvent and the material was embedded in a mixture of commercial Parowax and crude rubber³ and cut at 1 μ to 15 μ in thickness. 7 μ was found to be most satisfactory.

As a stain Heidenhain's Iron-Alum Haematoxylin gave the most satisfactory results. When counterstained, erythrosin was used. Triple stain was found to be inferior to Heidenhain's stain for this fungus.

Temporary mounts for supplementary study of all stages, from perithecial initials to crushed mature perithecia containing ascospores, were made in lactophenol and cotton blue.

² Division of Forest Pathology, Bureau of Plant Industry, in coöperation with the Forest Products Laboratory, Madison, Wis.

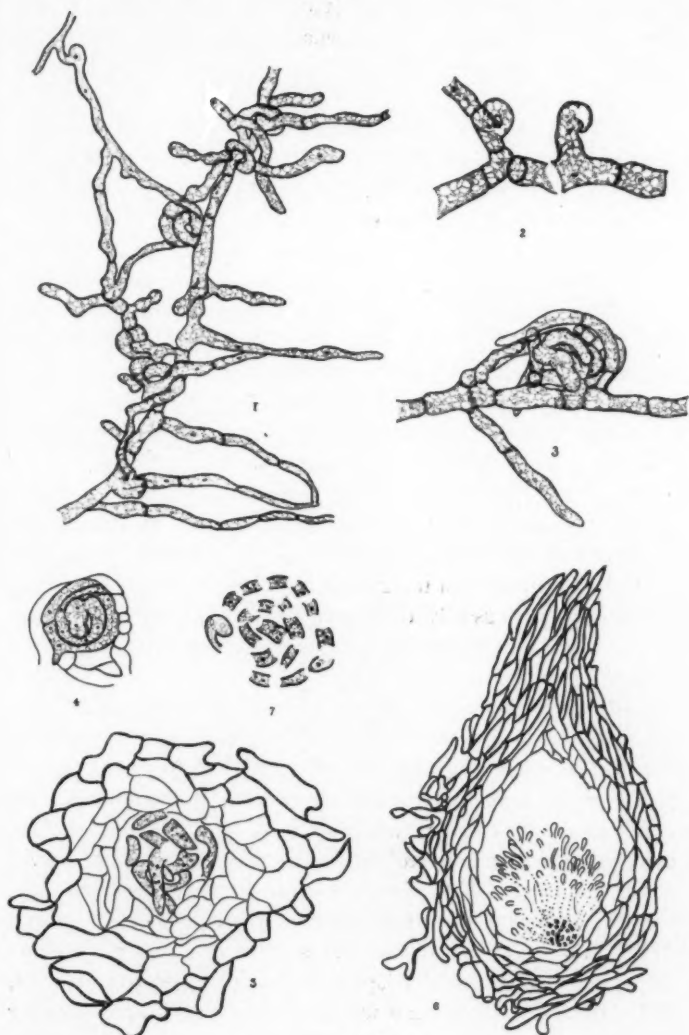
³ Stock—20 grams crude rubber and 100 grams Parowax. Use 5 grams stock with 100 grams Parowax for embedding.

MORPHOLOGY AND CYTOLOGY OF THE PERITHECIUM IN
CERATOSTOMELLA MONTIUM

The primordia of the ascocarps which give rise to perithecia may be recognized, microscopically, in culture, within forty-eight hours. The perithecia develop in small groups scattered about the plate and within seven days are visible to the naked eye. Within twelve days some of the perithecia can be seen to be maturing and, with a microscope, the beginnings of short necks are visible. Such perithecia usually produce long necks by the end of the month. It is to be noted that with the appearance of such maturing perithecia those immediately adjacent in each group cease development. It seems possible that such abortion may be related to food supply. It might be further pointed out that wherever large numbers of perithecia are produced there are frequently found sclerotial-like bodies having a slimy grey appearance. Microscopically these are seen to be composed of numerous tiny conidial-like spores. These spores differ, however, from the true conidia both in size and manner of production. The relation between these "microconidia" and perithecial production was not determined.

A perithecium originates as a short recurved branch on one of the vegetative hyphae (FIG. 2). No evidence of an antheridium has ever been encountered. The recurved branch continues to coil but soon becomes enveloped by branches which arise from adjacent cells (FIG. 3) forming a small knot. Several such knots usually develop in a series on any one hypha and occasionally such knots have been observed to end in long narrow cells which, at least superficially, resemble trichogynes (FIG. 1).

Each small knot consists of a sterile outer sheath and an inner fertile coil, the latter being derived from the enlargement and curvature of the original short recurved branch. The tip cell of the fertile coil is binucleate (FIG. 4). The origin of the binucleate condition was not determined. The coil soon becomes multinucleate (FIG. 7) through nuclear divisions not followed by cell divisions and from this coil there arise multinucleate ascogenous hyphae (FIG. 5). In most cases, with the development of the ascogenous hyphae, the coil is used up and, for this reason, the asci seem to come directly from the walls of the perithecium.



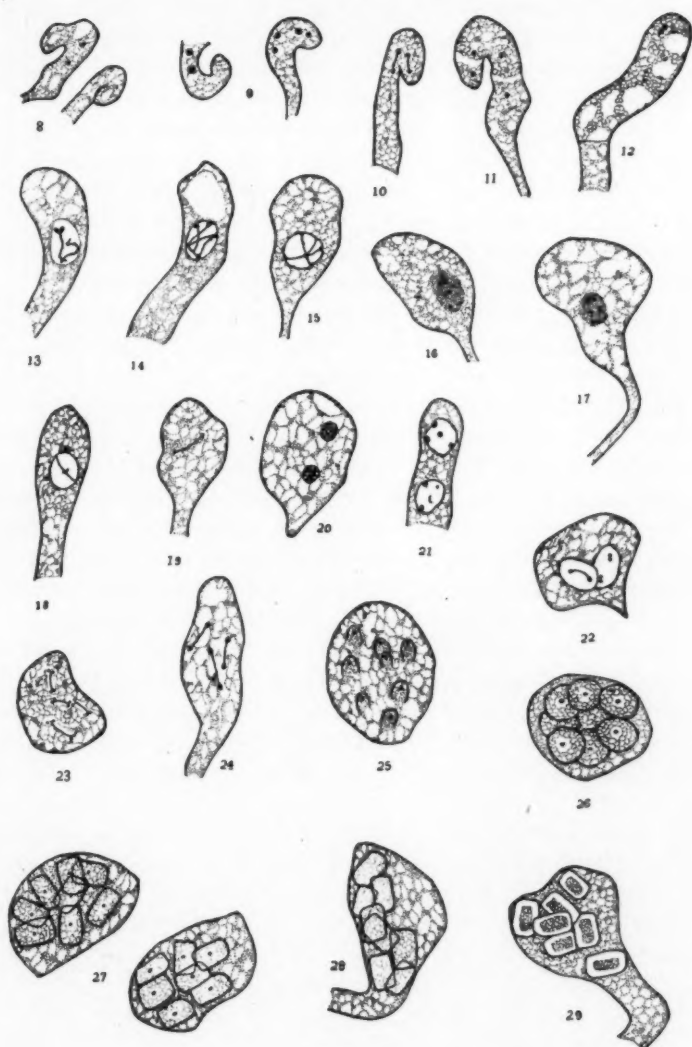
FIGS. 1-7.

However, the presence of a coil (FIG. 6, 7) at the base of a perithecium in whose cavity the ascogenous hyphae are producing asci suggests that certain cells of such a coil may well be the origin of the ascogenous hyphae.

Coincident with the development of the ascogenous hyphae there has been the development of a sterile sheath. The cells of the hyphal branches which had first enveloped the young coil increase in number, enlarge, and fuse so as to form a sheath of two layers about the coil (FIG. 5). The peripheral layer consists of dark brown, thick-walled cells which form a tough outer perithecial wall. The inner layer is pseudoparenchymatous in nature consisting of thin-walled, colorless cells. Occupying the central cavity of the perithecium lies the fertile coil embedded in a mass of thin-walled, cushion-like cells. These cushion cells break down readily coincident with the maturation of the fertile coil; it is assumed that the cushion cells perform a nutritive function. It is interesting to note that the cells of the outer brown sterile jacket frequently produce conidia, so that small clusters of conidia are commonly found around the perithecia. Small round cells identical in appearance with the conidia have been observed within the perithecial cavity, usually at the periphery. The vegetative hyphae which form the perithecial wall have apparently retained the capacity to produce conidia.

Within the perithecium the ascogenous hyphae begin the production of asci in typical fashion by the formation of croziers. The hyphae extend upward into the cavity, developing at the expense of the cushion cells, and spread out to partially fill the cavity in a somewhat bouquet effect (FIG. 6). The tips of these ascogenous hyphae are frequently seen to curve in typical crozier formation (FIG. 8-11). In these croziers, which are binucleate, nuclear divisions to form four nuclei have been observed (FIG. 10, 11). Two cross walls are then laid down which cut off a binucleate penultimate cell which develops into the primary ascus (FIG. 11, 12). In this young ascus a nuclear fusion occurs, and following this fusion the ascus enlarges considerably and is seen to contain the characteristic single, large primary nucleus (FIG. 13-15).

The primary nucleus of the ascus consists of chromatin material which strings across the central part of the nucleus and ends in



FIGS. 8-29.

small aggregations at the periphery (FIG. 13-15). In the pro-phases of the first division there are differentiated either four or six chromatin masses. The chromatin aggregations are so arranged that they may be interpreted either as six very small bodies, two pair of which are very close together, or as four bodies, two of which are bilobed (FIG. 16, 17). Following the first division (FIG. 18, 19) two nuclei are formed (FIG. 20) which undergo a second (FIG. 21, 22) and third division (FIG. 23, 24) to form eight nuclei. Such stages occur in rapid succession and are difficult to find; the uninucleate stage is the prolonged one. The small size of the chromatin masses made counts in the second and third divisions impossible. Following the production of eight nuclei, free cell formation occurs (FIG. 25). Because of the minute size of the nuclei the writer was unable to determine whether the nuclei were beaked or not. The spores are round when first cut out (FIG. 26) but later become polyhedral in shape (FIG. 27). Some of the ascus cytoplasm seems to remain as flanges on the spores. The spores are not subjected to much pressure within the ascus but rather lie free within that structure (FIG. 28). They readily undergo contraction and as a result often seem to consist of a narrow bar of protoplasm surrounded by a very thick transparent wall (FIG. 29); but in other cases they are seen to be well filled with protoplasm (FIG. 27). The ascus wall is very thin and, coincident with the enlargement of the ascospores, deliquesces leaving the spores lying free within the perithecial cavity (FIG. 30). Some enlargement of the spores occurs after their liberation from the ascus.

At some time previous to the production of the asci the pseudoparenchymatous cells in the upper part of the perithecium are seen to be growing. They turn upward and begin to elongate, pushing aside the outer sheath, which, however, is itself still capable of some growth in that region. These rows of elongate, narrow cells resemble an aggregate of vegetative hyphae. They continue to elongate ultimately forming a long neck. The outer hyphae of the neck resemble those of the outer layer of the perithecial wall being of the same dark brown color and having thick-walled cells. The inner hyphae consist of thin-walled hyaline cells like those of the pseudoparenchyma of the perithecium. By the time the

ascospores are mature the neck has reached its full length. The central hyaline cells then break down leaving a long central canal (FIG. 30). The perithecium now imbibes water and its contents begin to swell. A pressure is exerted which forces the perithecial contents up the canal of the neck and out of the ostiole. The disintegrated cells of the neck as well as some of the cellular remains of the perithecial cavity tend to hold the ascospores together in a sticky droplet at the tip of the neck.

DISCUSSION

Perithecial development in *C. montium* agrees in many respects with that in other species of this same genus. Although Varitchak reports the presence of an antheridium in the lumber blue stain fungus *C. Piceae* (13), it is to be noted that he considers it non-functional, and that he believes the ascogone originates as a binucleate structure; Andrus and Harter report a similar situation for the antheridium in *C. fimbriata* (2) whereas Gwynne-Vaughan and Broadhead (7) do not recognize even a non-functional antheridium. If the absence of an antheridium is to be considered an indication of reduction, then *C. montium* is certainly more reduced than *C. Piceae* and at least as reduced as *C. fimbriata* since it shows no evidence of an antheridium.

The origin of the binucleate condition in *C. montium* was undetermined. The fact that large numbers of perithecia are usually accompanied by the production of the aforementioned sclerotial-like bodies should not be lost sight of in the matter of possible explanations for such a binucleate condition. However, since there is at present no evidence to account for this binucleate condition, it is suggested that possibly in this species, as has been described for *C. Piceae* (13) and *C. fimbriata* (7), the binucleate condition arises as a result of a nuclear division not followed by septation.

C. montium resembles the other species of this genus in that the young fertile coil early becomes enveloped by a sheath resulting from the branching and fusion of hyphae which arise from cells adjacent to those which form the coil.

The multinucleate condition of the ascogenous hyphae presumably arises, as described in *C. fimbriata* (7), *C. Piceae* (13), *C.*

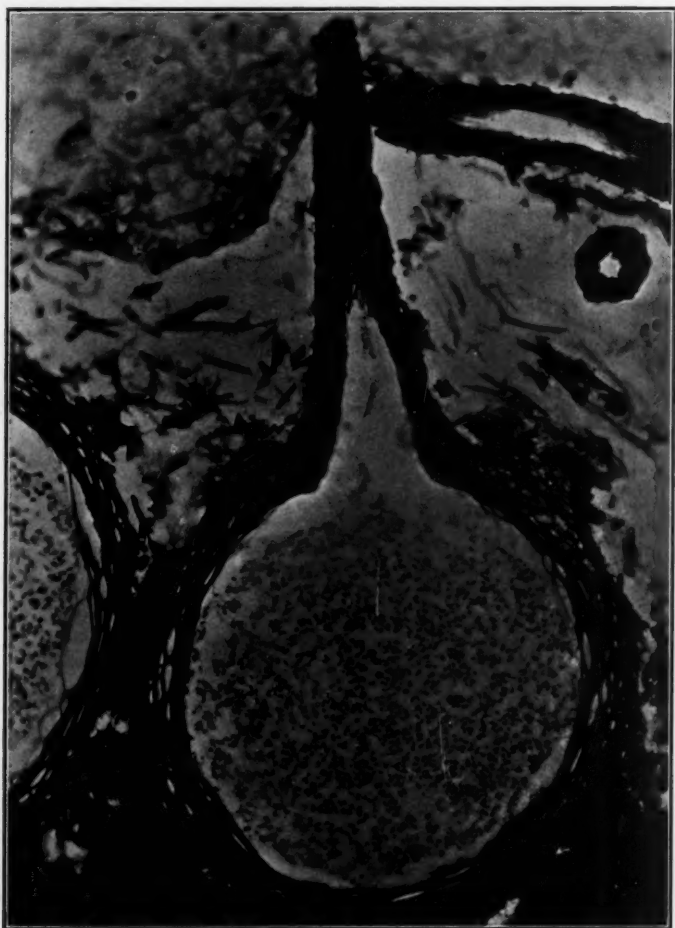


FIG. 30.

adiposa (12), and *C. multiannulata* (1), by a series of nuclear divisions not followed by cell divisions. Although the ascogenous hyphae seemed to present a naked condition as described by Andrus and Harter for *C. fimbriata* (2) and by Andrus for *C. multiannulata* (1), the presence of a wall in later stages of development

led the writer to assume that such apparently unvalled condition was due to protoplasmic contractions as suggested by Gwynne-Vaughan and Broadhead (7) for *C. fimbriata*.

In regard to the method of ascus formation *C. montium* agrees with those species in which typical crozier production has been described (7, 13). However, since there still seems to be some question as to whether crozier formation is the only method of ascus initiation in *C. fimbriata* (3), it may be that although typical croziers have now been reported in two of the blue staining members of the genus, in *C. fimbriata* (3) and in some of the other species (1, 2, 3) these stages have been somewhat modified.

Development within the ascus is of a typical ascomycetous nature. The three divisions appear normal. The number and appearance of the chromatin bodies resemble that found by Andrus and Harter in *C. fimbriata* (3). In no case was there any evidence of an ascus vesicle as described by Andrus and Harter for *C. fimbriata* (3); nor was the apparently naked condition of the asci as described for that same species and for *C. moniliformis* (3) and *C. multiannulata* (1) ever observed in *C. montium* although contractions of the cytoplasm often seemed to indicate that such was the case. Destaining to the point where nuclear structure was discernible often made both cytoplasm and wall very faint, especially when Heidenhain's Haematoxylin stain, which is essentially a nuclear stain, was used. As has been pointed out by Gwynne-Vaughan and Broadhead (7) well fixed and well stained preparations show the cytoplasm and wall to be normal.

Ascospores are produced in *C. montium* by typical free cell formation. No evidence of their developing as protuberances on a central protoplasmic mass, as described by Andrus and Harter (3), for *C. fimbriata* and *C. moniliformis* has ever been encountered. However, as described for those and other species of this genus (1, 2, 3, 7, 12, 13) the ascus wall of *C. montium* deliquesces early, frequently even before the spores have reached their mature size.

Although the development of the neck in *C. montium* was not followed in detail it follows in general that so adequately described by Sartoris for *C. adiposa* (12). As in *C. Piceae* (13) the outer cells of the perithecial wall of *C. montium* give rise to the outer cells of the neck.

In the liberation of its ascospores *C. montium* agrees with the condition found in *C. Piceae* (13) and *C. fimbriata* (7). As in other species of this genus (7, 12, 13) the ascospores are emitted in a gelatinous mass.

In conclusion the information concerning this new species of *Ceratostomella* might be summarized as follows. In respect to sex organs *C. montium* is less primitive than *C. Piceae* (13), *C. fimbriata* (2) (except according to the Gwynne-Vaughan and Broadhead (7) interpretation) or *C. multiannulata* (1) but perhaps not as reduced as *C. adiposa* (12) in that there is no antheridium but there is found a recurved initial comparable to an oogonium. In the development of its asci *C. montium* resembles especially *C. Piceae* (13) being similar in the production of croziers, neck formation, spore delimitation, and spore liberation. In "chromosome" number *C. montium* resembles *C. fimbriata* (3).

In general, from the foregoing observations, it would seem that *C. montium* is a typical ascomycete in its development.

SUMMARY

The fungus was cultured in petri dishes on a medium consisting of 4.15 per cent corn meal decoction and 1.5 per cent agar at 21° C.

The ascospores are produced in dark brown perithecia which have long necks from whose tips the spores are extruded as a gelatinous mass.

The perithecia often develop in groups but only a few of any one group ever mature.

Normal perithecial initials are visible, microscopically, in four to seven-day old cultures. Uninucleate asci begin their development within twelve days and perithecia mature within a month.

The perithecium begins as a recurved branch. No antheridium has ever been observed.

The recurved branch coils on itself and becomes the fertile coil of the young perithecium.

Cells immediately adjacent to those producing the fertile coil give rise to the sterile sheath.

The cells of the fertile coil become multinucleate by nuclear divisions not followed by cell divisions.

Some cells of the fertile coil give rise to ascogenous hyphae at whose tips asci are formed by typical crozier development.

Asci are produced successively by the ascogenous hyphae.

The primary nucleus of the ascus shows strands of chromatin material which tends to aggregate at the periphery of the nucleus.

In the prophase of the first division either four or six chromatin aggregations are visible.

Within the ascus three nuclear divisions produce eight nuclei about which spores are delimited by free cell formation.

The spores are round when first cut out but they later take on a polyhedral shape bearing flanges which seem to be cytoplasmic remnants.

Coincident with, or shortly before, the time the spores reach their full size the ascus wall disappears leaving the spores lying free in the perithecial cavity.

The perithecial sheath consists of two zones—an outer layer of dark brown, thick-walled cells and an inner pseudoparenchymatous layer of thin-walled cells.

At the time the ascogenous hyphae are developing beak formation begins. By the time the ascospores are mature this beak has elongated into a neck whose inner cells break down to allow for the escape of the spores.

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BOTANY DEPARTMENT,
UNIVERSITY OF WISCONSIN,
MADISON, WISCONSIN

LITERATURE CITED

1. Andrus, C. F. Cell relations in the perithecium of *Ceratostomella multiannulata*. Mycologia 28: 133-153. 1936.
2. Andrus, C. F. & Harter, L. L. Morphology of reproduction in *Ceratostomella fimbriata*. Jour. Agr. Res. 46: 1059-1078. 1933.
3. —. Organization of the unwalled ascus in two species of *Ceratostomella*. Jour. Agr. Res. 54: 19-47. 1937.
4. Butler, E. J. Fungus diseases of sugar cane in Bengal. India Dept. Agr. Mem. Bot. Ser. 1st: 1906.
5. Elliott, J. A. The ascigerous stage of the sweet potato black-rot fungus. (Abstract.) Phytopath. 13: 56. 1923.
6. —. A cytological study of *Ceratostomella fimbriata*. Phytopath. 15: 417-422. 1925.
7. Gwynne-Vaughan, H. C. I. & Broadhead, Q. E. Contributions to the study of *Ceratostomella fimbriata*. Ann. Bot. 50: 747-759. 1936.
8. Halsted, B. D. Some fungous diseases of the sweet potato. N. J. Agr. Exp. Sta. Bull. 76. 1890.
9. Halsted, B. D. & Fairchild, D. O. Sweet potato black rot. Jour. Myc. 7: 1-11. 1891.
10. Mittmann, C. Kulturversuche mit Einsporstämmen und zytologische Untersuchungen in der Gattung *Ceratostomella*. Jahrb. Wiss. Bot. 77: 185-219. 1932.
11. Rumbold, C. *Ceratostomella montium* n. sp., a blue stain fungus associated with two species of *Dendroctonus*. (In press.) 1940.
12. Sartoris, G. B. A cytological study of *Ceratostomella adiposum* (Butl.) comb. nov., the black-rot fungus of sugar cane. Jour. Agr. Res. 35: 577-585. 1927.
13. Varitchak, B. Contribution à l'étude de développement des Ascomycètes. Le Bot. 23: 1-142. 1931.

EXPLANATION OF FIGURES

FIGS. 1-29. Drawings were made with the aid of a Spencer camera lucida at table level. Reduction of all figures ca. $\frac{1}{8}$.

FIG. 1, young perithecial knots (ca. $\times 520$); 2, perithecial initials ($\times 1040$); 3, young fertile coil being enveloped by sheath hyphae which are developing from adjacent hyphal cells ($\times 1040$); 4, cross section of young knot containing binucleate tip cell and showing multinucleate condition of rest of coil. Sheath cells are at periphery ($\times 1460$); 5, multinucleate ascogenous hyphae which have developed from the fertile coil. Sterile sheath shows considerable development ($\times 1040$); 6, young perithecium in which asci are being formed in the center of the cavity. At the base is a persistent fertile coil. Opposite the coil is the elongating neck. The perithecial sheath shows two zones ($\times 220$); 7, enlargement of the fertile coil observed at the base of the perithecium shown in Fig. 6 ($\times 1040$).

FIGS. 8-29. All drawings are $\times 1860$. FIGS. 8-11, stages in crozier formation; 10, division in the crozier to form four nuclei; 11, four nucleate crozier; 12-15, primary asci; 13-15, nuclei of primary asci showing arrange-

ment of chromatin material; 16, 17, prophases of the first division showing chromatin aggregations which may be interpreted either as six very small bodies or as four, two of which are bilobed; 18, 19, first nuclear division in the ascus; 20, binucleate ascus; 21, prophases of the second nuclear division in the ascus; 22, second nuclear division in the ascus; 23, 24, third nuclear division in the ascus; 25, free cell formation in the ascus; 26, spores as cut out in the ascus are, at first, round; 27, spores becoming polyhedral; 28, spores lying free in the ascus—show no evidence of pressure; 29, spores in the ascus showing the peculiar bar of protoplasm due to contraction.

FIG. 30. Photomicrograph. Longitudinal section through mature perithecium showing cavity filled with polyhedral ascospores. The thick walled sheath can be seen at the periphery and at the top is the neck with its open canal. ca. $\times 250$.

THE GENUS *ARMILLARIA* IN WESTERN WASHINGTON

H. H. HOTSON

(WITH 3 FIGURES)

The genus *Armillaria* is well represented in western Washington, some species occurring very abundantly, especially *Armillaria mellea*. The genus was first recognized by Fries in 1821 (4) as a tribe under *Agaricus* but later it was discarded by both Ricken and Lange who distributed the species among other genera. In 1914, Ricken (23) in his reorganization of the genus, transferred seven species, including *Armillaria mellea*, to the genus *Clitocybe*, nine to *Tricholoma*, three to *Collybia*, and four to *Pleurotus*. In 1914, Lange (18) in general followed Ricken's interpretation of the genus but placed *Armillaria mellea* in the genus *Lepiota*.

In America most mycologists have not accepted this abolition of the genus for, although admitting it to be a more or less heterogeneous group, they believe that transferring the various species to other genera does not solve the problem. Peck (21), in 1890, describes eight species which, at that time, were known in the United States. Murrill (20), in 1914, listed 14 species, two of which were tropical. He only included three of Peck's eight and left the others unmentioned. Kauffman (13), in 1918, described six species, two of which, *A. dryina* and *A. corticata*, had previously been placed in the genus *Pleurotus*. Again, in 1922, he (15) consolidated the genus for the United States and listed 28 species, eleven of which have been reported for Washington and Oregon, and two of which have later, due to the work of Zeller, been proven to be synonymous, *A. ponderosa* and *A. arenicola* (27). Since that time five additional species have been reported by Zeller and Kauffman for Washington and Oregon. In the present article, which is the fourth of a series on the Agaricaceae of Western Washington (10, 11, 12), fifteen species are reported.

The writer has two main objects in view in this article: to bring

together the scattered information regarding the genus as it occurs in the Pacific Northwest; and to put this and any new information into a usable form so that it may be a basis for further study of the genus. To this end a key has been constructed similar to that given in another article (12), which combines the usual skeleton key with a more or less complete description of each species in order to facilitate their identification.

There is some difference of opinion among mycologists as to the exact limits of this genus. Certain species seem to be transitional forms having certain characteristics of *Armillaria* and others of the genus *Lepiota*. *Armillaria* is described as having an annulus and attached gills, and *Lepiota* an annulus and free gills. *A. granosa* and *A. amianthina* (which were formerly placed in the genus *Lepiota*) have an annulus and attached gills, while in other respects they are like *Lepiota*. Kauffman quite logically has transferred such forms to the genus *Armillaria* and in this paper his interpretation has been accepted. There are a few species, such as *A. dryina* and *A. corticata*, commonly placed in the genus *Pleurotus* because of their eccentric or lateral stems, which have a ring and the gills attached or decurrent. Following Kauffman's suggestion, these have been placed in the genus *Armillaria*, also. Thus, any white-spored form with attached or decurrent gills, with the stem and pileus continuous, having a ring but lacking a volva, is considered to belong to the genus *Armillaria*.

ARMILLARIA Fries, Syst. Myc. 1: 26. 1821

(From the Latin, *armilla*, a ring, referring to the presence of the annulus)

Pileus fleshy, regular; *gills* adnexed, adnate or decurrent, sometimes with a diverging trama; *stem* fleshy, continuous with the pileus, central or lateral; *annulus* present, persistent, membranous or subarachnoid; *spores* white in mass, smooth; growing on the ground or on wood, mostly in the autumn; often compact, firm mushrooms; sometimes caespitose.

In structure this genus resembles *Pholiota* among the ochra-spored, and *Stropharia* of the purple-brown-spored species.

KEY TO THE SPECIES OF *ARMILLARIA*

A. Stem lateral or eccentric; pileus white or whitish.

B. Spores oblong $9-10 \times 4-4.5 \mu$, smooth and white; gills not anastomosing at stem, decurrent, white, broadest in the middle; pileus white, 4-8 cm. broad, firm, floccose at first, becoming scaly from the breaking up of the floccose covering, scales darkening with age, margin at first involute; stem lateral or eccentric, 2-4 cm. long, 1-1.5 cm. thick, sometimes becoming densely hairy, especially toward the base; annulus somewhat evanescent; veil thin and membranous; odor strong of bitter almonds. 1. *A. dryina* (Fries) Pat.

BB. Spores cylindrical $13-17 \times 4-5 \mu$, smooth and white; gills anastomosing at the stem, decurrent, narrowed toward the stem, white becoming yellowish, edge entire; pileus 6-15 cm. or more broad, convex-expanded, obtuse or depressed, firm, dull white or becoming brownish, finely floccose at first, cuticle breaking up into scale-like areas, margin involute at first; stem 4-10 cm. long, eccentric, sometimes stout and short, solid, firm, subtomentose or floccose, reticulate in large specimens; annulus thin, white floccose-membranous, evanescent; odor disagreeable. 2. *A. corticata* (Fries) Pat.

AA. Stem central or nearly so.

C. Gills decurrent, sometimes adnate, whitish or dingy yellow, becoming rusty with age, often powdery white due to the spores; pileus 3-10 cm. or more broad, oval, becoming convex to almost plane, usually honey-colored, varying to yellowish-brown or pale covered with dark-brown or blackish pointed scales, margin striate in age, context white; stem variable in length, 5-15 cm. long, 6-20 mm. thick, equal, stuffed becoming hollow, elastic, floccose scaly, whitish above, dingy yellow, brownish or rusty-stained below; annulus superior; veil usually well developed, membranous, both veil and annulus sometimes evanescent; spores elliptical-ovate, $8-9.5 \times 5-6.5 \mu$, white, smooth, nucleate; taste somewhat disagreeable or acrid. 3. *A. mellea* Fries.

CC. Gills variously attached but not decurrent (exc. *A. granulosoides* sometimes)

D. Pileus granulose or granulose-warty

E. Gills adnate

F. Disc of the pileus rugose

G. Growing on rotten wood or stumps; pileus 5-9 cm. broad, ovate, then convex-expanded, umbonate or obtuse, ochraceous to cinnamon-brown, furfuraceous-granulose, rugose-wrinkled to almost even, margin regular or undulate, context thick, white or slightly ochraceous; stem 5-10 cm. long, 8-15 mm. thick, equal or tapering upward from the clavate base, peronate by furfuraceous or floccose scale, colored like the pileus; annulus membranous, large, flaring, persistent; gills crowded, adnate, sometimes subarcuate, whitish to ochraceous; spores smooth, $4-5 \times 3 \mu$. 4. *A. granosa* Kauff.

GG. Growing on the ground; pileus 1-4 cm. broad, rugose-reticulate, cinnamon-brown on the disc, antimony-yellow to ochraceous on the margin, not umbonate, context thick and white; *stem* 4-7 cm. long, 3-4 mm. thick, equal or tapering upward, solid, peronate with cinnamon or reddish-brown floccose scales; *gills* adnate, sometimes subdecurrent, crowded, white, edge entire; *spores* $4-5.5 \times 3 \mu$, smooth, ovoid, apiculate, white; *annulus* incomplete or evanescent.

5. *A. rugoso-reticulata* Zeller.

FF. Pileus not rugose, 2-6 cm. broad, ovoid to campanulate and convex-expanded, subumbonate, surface finely to coarsely granulose, ochraceous to reddish-ferruginous varying to pallid or pinkish, context thin, white or yellowish; stem subequal, 4-8 cm. long, 2-7 mm. thick, whitish at the apex, covered with ochraceous granules below the annulus; annulus membranous, large; veil lacerate more or less appendiculate; gills adnexed to adnate, at times apparently free, rather broad, close, white becoming yellowish; spores $3-7 \times 2.5-4 \mu$, elliptical or subglobose, smooth, white; odor disagreeable.

6. *A. amianthina* Kauff.

EE. Gills adnexed

H. Pileus ochraceous or rusty-brown becoming paler when dry, 3-6 cm. broad, ovate becoming convex-expanded, or subumbonate, furfuraceous-granular, often radiately wrinkled, context thin, yellowish white becoming reddish; stem 2-5 cm. long, 4-8 mm. thick, stuffed to hollow, equal or tapering upward, granulose to floccose-scaly and reddish below the annulus, whitish at the apex; annulus slight, evanescent; gills adnexed, rounded at the stem, white; spores $4-5 \times 3-3.5 \mu$, ovate, smooth; cystidia none.

7. *A. granulosa* Kauff.

HH. Pileus cinnabar-red or rusty red, 5-8 cm. broad, convex to plane, obtuse, furfuraceous-granulose, margin fimbriate, context ochraceous, reddish under the cuticle of the pileus and stem; stem 4-7 cm. long, 1-2 cm. thick, equal or tapering upwards, covered with reddish granules below the ring; gills white, adnexed, sometimes nearly free; annulus concolorous, thin, narrow, inferior, evanescent; spores white, elliptical, obtuse, $4 \times 2.5-3 \mu$, one-guttulate; cystidia hair-like, acute.

8. *A. cinnabarina* Kauff.

DD. Pileus not granulose or granulose-warty

I. Pileus 2-6 cm. Broad

J. Spores $3-4.5 \times 2-3 \mu$, elliptical, white, often adhering in groups of two, three, or four; pileus 2-5 cm.

broad, convex, expanding to plane and usually depressed in center, surface squamulose scaly, light ochraceous-buff to tawny, sometimes staining almost russet, cream to buff between the scales, context thin, white, to creamy; *stem* 2-5 cm. long, 2-4 mm. thick, rufescent to tawny above and below, peronate with floccose to subfloccose scales; *gills* broad, adnate to slightly decurrent, often breaking away, white to creamy, edges even; *annulus* superior, thin, small, evanescent.

9. *A. granuloides* Zeller.

- JJ. **Spores 5.5-7 × 5-6 μ, oblong to subglobose, white;** *pileus* 4-6 cm. broad, convex to plane, slightly umbonate, surface dry, squamulose on disc to fibrillose-scaly toward margin, bay to brown on the disc, to light ochraceous-salmon towards the margin, context rather thin at margin, thick at the disc, white to creamy, slowly becoming pinkish when exposed; *stem* hollow, 5-7 cm. long, 8-12 mm. thick, striately fibrillose scaly; *gills* white, becoming pinkish, adnate, edges even; *annulus* fugaceous, arachnoid; *odor* and *taste* slightly farinaceous.

10. *A. badicephala* Zeller.

II. **Pileus usually much larger**

- K. **Pileus white, creamy-white or buff; not with marked yellow or red shades**

L. **Odor strong, penetrating, subalkaline; spores ellipsoidal, 5-6 × 3-3.5 μ; pileus** fleshy, 6-15 cm. broad, compact, convex to plane, glabrous, whitish with a slight yellowish or reddish-yellow tint, margin at first incurved and tomentose, context compact, white; *stem* equal, 4-10 cm. long, 2-3 mm. thick, solid, firm, sheathed at first with a thin membranous veil; *gills* narrow, crowded, sinuate, adnate or subdecurrent, whitish; *annulus* whitish above, narrow, membranous, more or less flaring.

11. *A. viscidipes* Peck.

- LL. **Odor mild; spores white, smooth, subglobose to oblong, 5-6 × 4.5-5 μ; pileus** 8-21 cm. broad, thick, firm, convex or broadly umbonate to gibbous, nearly plane when expanded, dry to subviscid, glabrous becoming fibrillose, at first white or pinkish buff, disc becoming light ochraceous-salmon, margin white to creamy, inrolled, context white, firm; *stem* 10-15 cm. long, 3-4 mm. thick, cylindrical or tapering downward, smooth below, somewhat scaly above the annulus; *gills* emarginate, becoming sinuate-adnexed or breaking free at maturity, whitish to light buff becoming warm buff, changing to brown when bruised; *annulus* ample, persistent, membranous.

12. *A. ponderosa* (Peck) Sacc.

KK. Pileus with marked yellow or red shades

M. Pileus apricot-yellow to yellowish brown, darker at the center, viscid, 5-10 cm. broad, tinged tawny in age, convex to expanded, umbonate, margin thin, slightly repandent, smooth; stem 6-8 cm. long, 8-12 mm. thick, straight, even, stuffed-hollow, coarsely floccose, woolly up to the annulus, white, smooth above; gills thin, sinuate-adnate to adnexed, white becoming pale yellow; spores white, smooth, subelliptical, $4-6 \times 3-4 \mu$; veil present when young, persisting as an inconspicuous annulus. 13. *A. albolanaripes* Atk.

MM. Pileus with reddish-brown or reddish-orange shades

N. Pileus covered with tawny-orange to ochraceous-rufous scales, 5-7 cm. broad, convex then expanded, subumbonate, with a pellicle which soon breaks into numerous crowded scales, margin at first inrolled and glutinous-floccose, context white, thin on the margin; stem 4-7 cm. long, 8-15 mm. thick, solid, equal or tapering downward, covered by concolorous scales up to the evanescent annulus, white at apex and between scales; gills rounded near the stem, slightly adnexed, white, spotted rusty-brown in age, some forked, edge entire; spores globose-oval, variable, $4-5 \times 3-4 \mu$, smooth, nucleate, white; odor strongly farinaceous, somewhat disagreeable.

14. *A. aurantia* Fries.

NN. Pileus glabrous (sometimes innate-fibrillose), compact rimose, viscid when wet, 7-15 cm. broad, margin somewhat revolute, undulate at maturity, and slightly exceeding the gills, disc ochraceous-tawny to brown with orange spots, a light pale-tan toward the margin, context white, thick at the disc; stem cylindrical or tapering downward, 6-15 cm. long, 1.5-3.7 cm. thick, scaly below, squamulose above, creamy, stained reddish-brown where bruised; gills 1 cm. broad, whitish becoming ochraceous-tawny at maturity, drying various shades of buff, darker where bruised, edges entire to wavy; annulus superior, fibrose-membranous; spores ellipsoid to ovoid, $6-7.5 \times 3.5-5 \mu$, white.

15. *A. robusta* (Alb. & Schw.) Fries.

DISCUSSION

1. *Armillaria dryina* (Fries) Pat. Tax. Hymén. 156. 1900.
Syn.: *Pleurotus dryinus* Fries, Syst. Myc. 1: 180. 1821;
Hymen. Eur. 167. 1874.

Although this species has been reported in eastern United States occurring on stumps and logs, the collections in Washington have been mainly in the ground in wet ravines. As suggested by Kauffman (15), this might account for the unusual tomentose character of the stem. It has the general appearance of *Pleurotus* in which genus it was formerly placed, but with the present conception of the genus *Armillaria* it should logically be placed in that genus. It is characterized by a strong odor of benzaldehyde (bitter almonds) and has a flat unpleasant taste.

Collected in a ravine near Richmond Beach, Oct. 15, 1939.

2. *A. corticata* (Fries) Pat. Tax. Hymén. 156. 1900.
Syn.: *Pleurotus corticatus* Fries, Syst. Myc. 1: 179. 1821;
Hymen. Eur. 166. 1874.

This species was first found in the Pacific Northwest in Oregon by S. M. Zeller in 1922 (25). It is not common. I have not been able to find any in the field but have had access to specimens in the herbarium. This species has an eccentric stem resembling *Pleurotus*, but as it has a ring with the pileus and stem continuous, and the spores white, it has been placed in the genus *Armillaria*. It is very similar to *A. dryina* and Atkinson (1, p. 106) has considered it merely as an ecological form. Kauffman, however, found a difference in the size of the spores and considered it a separate species. Schroeter gives the size of the spores as $13-15 \times 4-5 \mu$ and our herbarium specimens come within that range.

3. *A. mellea* Fries, Syst. Myc. 1: 30. 1821.

This species is very common around Puget Sound and is the most outstanding one of the entire genus. It has no close relation to any other form and can readily be recognized by the decurrent gills. It is often known as the "Honey Mushroom," and the "Honey Agaric" on account of the yellowish pileus. It is extremely variable in its characters and seems to combine some of

the features of many of the *Agarics*. It is of economic importance in that it causes a root rot of both trees and shrubs in the forest and in the orchard. The fungus which attacks conifers does not seem to attack fruit trees and vice versa, suggesting that there are two strains of mycelia. However, no distinction in the sporophores can be seen. It is found in caespitose clusters at the base of living trees and is parasitic on the roots. It forms very pronounced rhizomorphs which are easily found in the immediate vicinity of the sporophores.

The rhizomorphs have been found very abundant in certain wells in the vicinity of Seattle forming mats of intertwining black threads in the water. They have also been found in masses hanging from decaying timber supports in mines. An examination of these rhizomorphs in relation to the plants which they attack indicates that they are capable of gaining entrance to the host by a sort of mechanical pressure rather than by an enzyme.

4. *A. granosa* (Morg.) Kauff. Papers Mich. Acad. Sci. 2: 60. 1922.

Syn.: *Lepiota granosa* Morg., Myc. Flora Miami Valley 2: 63.

The umbo of this species is round and small, but definite. The margin of the pileus is even and does not exceed the gills. The surface is granular especially on the umbo and growing less dense toward the margin. In older specimens the surface of the margin may not be granular. When young, the center of the pileus is uniformly ochraceous but later it becomes auburn shading through Sanford-brown to tawny, ochraceous tawny or even buff on the margin.

The universal veil covers the entire lower half of the stipe forming a definite membranous sheath whose upper end flares out and up into a broad conspicuous collar, the annulus. This sheath is just like a close fitting boot and can be peeled off of the stem with ease. It is the character of this persistent annulus which makes it fairly easy to distinguish this species.

It is not very common around Seattle and does not entirely agree with Kauffman's description of the species. It is similar to *A. amianthina* but is larger and the annulus is more pronounced. It has been collected on the Tacoma "prairies" and on San Juan Island.

5. *Armillaria rugoso-reticulata* (Lorin) Zeller, *Mycologia* 25: 378. 1933.

Syn.: *Lepiota rugoso-reticulata* Lorin, *Oesterr. Bot. Zeits.* 1879.

This species resembles *A. granulosa* in color but differs in its slender stem and rugose pileus. It approaches *A. granosa* in the character of the pileus but it is small and the annulus is rarely persistent. It differs from *A. amianthina* in the lack of an umbo and small spores. The spore measurements follow very closely those reported by Zeller, $4-6 \times 3-3.5 \mu$.

This species is rather rare. The specimens examined showed the rugose pileus very clearly, especially when young. The pileus measures up to 3 cm. broad; convex to campanulate becoming expanded and later plane sometimes with a small, shallow umbo. It exceeds the gills by about one mm. or less and is always conspicuously appendiculate with more or less triangular patches. The color when very young is Sudan brown, becoming near Buchthorn brown but darker, eventually becoming uniformly an antimony yellow.

6. *Armillaria amianthina* (Fries) Kauff. *Papers Mich. Acad. Sci.* 2: 60. 1922.

Syn.: *Lepiota amianthina* Fries, *Monog. Hymen. Suec.* 1: 29. 1857; *Hymen. Eur.* 27. 1874.

The surface of pileus of this species is characteristically granulose although it may vary in color. It is found very commonly on the San Juan Islands on coniferous logs, in moss, under vine maple, Douglas fir, hemlock, and spruce. The color variation apparently is due to the environment in which it grows. When growing in very moist places under trees the pigments are intense while in the open the pigments seem to be bleached out and the color is much lighter.

In the specimens collected, the pileus has not exceeded 4.5 cm. broad and is obtusely convex but not definitely umbonate. The margin at first somewhat exceeds the gills and tends to form triangular appendiculate flaps in some of the specimens, but it becomes incurved and wavy with age. The surface is densely granulose and sometimes finely, radially rugose on the margin extending

about half way to the center of the pileus. The young specimens have the center of the pileus a Buckthorn brown with the margin antimony yellow; in the older specimens the center is ochraceous tawny while the margin is ochraceous buff. The gills are squarely



FIG. 1. *Armillaria amianthina*.

adnate, broad and pointed at the margin alternating long and short. The stem varies from 3-6 cm. long and 3-6 mm. thick. It is cylindrical, equal to slightly thickened toward the base, hollow, and fibrous. The surface is floccose-granular on the lower half and fibrous on the upper portion. It ranges from Buckthorn brown below to ochraceous buff above, becoming Sayal brown with age.

7. *Armillaria granulosa* (Fries) Kauff. Papers Mich. Acad. Sci. 2: 60. 1922.

Syn.: *Lepiota granulosa* Fries, Syst. Myc. 1: 24. 1821.

This species is not very common in the Pacific Northwest. It has been collected on San Juan Island among moss under Douglas fir trees. It resembles *A. amianthina*, *A. granosa*, and *A. rugoso-reticulata* but is distinguished from all of them by the attachment of the gills which are adnexed. This seems to be the main distinguishing character of the species although the pileus is rather striking in color being ochraceous and tinted brick red.

8. *Armillaria cinnabarina* (Fries) Kauff. Papers Mich. Acad. Sci. 2: 60.

Syn.: *Lepiota cinnabarina* Fries, Monog. Hymen. Suec. 1: 29. 1857; Hymen. Eur. 36. 1874.

This species is extremely rare in the Pacific Northwest. It has been collected on Mt. Hood, Oregon, by Kauffman (15) and by the writer on San Juan Island and near Index, Washington.

There is a question as to whether this species should be included in this genus. The gills range from nearly free to distinctly adnexed but at times they are definitely free. This factor would eliminate it from this genus except that the specimens with the free gills are very much in the minority. I have found only one whose gill-attachment could be called free.

9. *Armillaria granulosoidea* Zeller, Mycologia 25: 377. 1933.

This species was first reported by Zeller in Oregon in 1933 (25) and due to its resemblance to *A. granulosa* he named it *A. granulosoidea*. It grows consistently in mossy places, sometimes in the open and sometimes along the edge of Douglas fir timber. The writer has collected it around Chase Lake and near Richmond Heights, Washington.

10. *Armillaria badicephala* Zeller, Mycologia 27: 459. 1935.

This species was reported first in Oregon by Zeller in 1935 (28). It has the general appearance of *Tricholoma*. Our specimens fit exactly the description given by Zeller. Found chiefly in coastal regions but also inland around lake and coniferous wood region. Collections were made by the writer in the vicinity of Chase Lake, Washington.

11. *Armillaria viscidipes* Peck, N. Y. State Mus. Bull. 44: 15. 1891.

In 1922, Kauffman found this species on Mt. Hood, Oregon (14, 15). He made a careful study of it as it occurs in the Pacific Northwest and suggests some modifications of Peck's original description. The spores are slightly smaller than the size given by Peck. The gills are adnate at first, becoming "slightly acuminate-decurrent" and sinuate in old plants.

12. *Armillaria ponderosa* (Peck) Sacc. Syll. Fung. 5: 58. 1887.
Syn.: *Armillaria magnivelaris* (Peck) Murr. N. Am. Flora 10:
37. 1914.

Armillaria arenicola Murr., Mycologia 4: 212. 1912.

This species is usually found in sandy soil, either in the open or under pine or Douglas fir. It has been collected near Port Angeles, on Bainbridge Island and on San Juan Island. Zeller (27) has



FIG. 2. *Armillaria ponderosa*.

described this species quite thoroughly and compared it with *A. magnivelaris* (Peck) Murr. and also with a closely related Japanese species *A. matsutake* Ito & Imai. See his article for further details (27).

13. *Armillaria albolanaripes* Atk. Ann. Myc. 6: 54. 1908.

This species has been collected in Oregon and Washington by Zeller (25) and also by Kauffman (14, 15). The writer has found it rather sparingly in the low lands of Snohomish County, Washington, under conifers in late November. The species may be recognized by the bright yellow or yellowish-brown color of the pileus which is darker at the center.

14. *Armillaria aurantia* Fries, Syst. Myc. 1821.

Syn.: *Tricholoma aurantium* Fries, Hymen. Eur. 41. 1874.

As has been mentioned, *A. dryina* and *A. corticata* resemble rather closely *Pleurotus* and *A. granosa* and *A. granulosa* seems

related to *Lepiota*, so in *A. aurantia* we find a species approaching very closely to *Tricholoma*. Kauffman, in his *Agaricaceae* of Michigan (13), describes it as an *Armillaria* while in a later article (15) he places it among the "Doubtful Species."



FIG. 3. *Armillaria aurantia*.

It is evidently on the borderline between the two genera. It has a veil but it seldom leaves an annulus. The gills are sinuate or emarginate and the structure of the trama is similar to *Tricholoma*. The gills, however, are adnexed although very slightly in some specimens. This adnexed condition of the gills is about the only excuse for placing it in the genus *Armillaria*, yet if we adhere strictly to the characteristic of the genus as already stated, that the gills of *Armillaria* may be "adnexed, adnate or decurrent," then it would seem that this is the proper place for it. There is room, however, for difference of opinion in regard to this species.

15. *Armillaria robusta* Fries, Hymen. Eur. 41. 1874; Sacc. Syll. Fung. 5: 74. 1887.

Zeller (29) gives a detailed description of this species as it occurs in the Pacific Northwest. It grows under much the same conditions as *A. ponderosa* but is readily distinguished from it by the reddish or cinnamon color of the pileus and the orange spots on the disc. It is fairly common along the Coastal Regions of Washington during October and November (29).

The description in the key is adapted from Zeller's (25).

ACKNOWLEDGMENTS

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DEPARTMENT OF BOTANY,
UNIVERSITY OF WASHINGTON,
SEATTLE, WASHINGTON

BIBLIOGRAPHY

1. Atkinson, G. F. The development of *Armillaria mellea*. Myc. Contrbl. 4: 113. 1914.
2. —. Mushrooms. 1900.
3. Bresadola, A. J. Iconographia mycologica 1: pl. 44-50. 1927.
4. Fries, Elias M. Systema mycologicum. 1821.
5. —. Epicrisis Sys. Myc. 1836-38.
6. —. Hymenomycetes Europaei. 1874.
7. —. Monographia Hymenomycetum Sueciae. 1857-63.
8. —. Icones. 1867-1884.
9. Henning (Engler & Prantl), vol. 1, part 1—No. 2, p. 231 and p. 269-273. 1897.
10. Hotson, J. W. & Lewis, Esther. *Amanita pantherina* of western Washington. Mycologia 26: 384-391. 1934.
11. —. The Amanitae of western Washington. Mycologia 28: 63-76. 1936.
12. — & Stuntz, D. E. The genus *Agaricus* in western Washington. Mycologia 30: 204-234. 1938.
13. Kauffman, C. H. Agaricaceae of Michigan 1: 1918.
14. —. Fungous flora of Mt. Hood. Papers Mich. Acad. Sci. 5: 124. 1925.
15. —. The genus *Armillaria* in the United States and its relationships. Papers Mich. Acad. Sci. 2: 53-67. 1922.
16. —. Papers Mich. Acad. Sci. 4: 311-344. 1924.
17. Kaufert, F. The production of asexual spores by *Pleurotus corticatus*. Mycologia 27: 333-34. 1935.
18. Lange, J. E. Flora Agaricina Danica 1: 39. 1935.
19. Murrill, W. A. The Agaricaceae of the Pacific Coast. Mycologia 4: 212. 1912.
20. —. N. Am. Flora 10: 36. 1914.
21. Peck, C. H. N. Y. State Mus. Rep. 43: 86. 1890.
22. Rea, C. British Basidiomycetes, p. 105-110. 1922.
23. Ricken, A. Die Blotterpilze Deutlands 1: 329; 361; 400. 1914.
24. Saccardo, P. A. Sylloge fungorum 5: 73-87. 1886.

25. Zeller, S. M. Contributors to our knowledge of Oregon fungi—I. *Mycologia* 14: 173-199. 1922.
26. —. New or noteworthy Agarics from Oregon. *Mycologia* 25: 376-391. 1933.
27. — & Togashi, K. The American and Japanese Matsu-takes. *Mycologia* 26: 550. 1934.
28. —. Some miscellaneous fungi of the Pacific Northwest. *Mycologia* 27: 459. 1935.
29. Zeller, S. M. New and noteworthy agarics from the Pacific Coast States. *Mycologia* 30: 472. 1938.

STUDIES IN THE PATELLARIACEAE

ELLYS THEODORA BUTLER

(WITH 10 FIGURES)

INTRODUCTION

The task of monographing the North American species of the Patellariaceae was undertaken with the understanding that this family included a group of inoperculate Discomycetes, of the order Pezizales. Two interesting observations have greatly modified the course of this study. First, the discovery of a type of ascus dehiscence characteristic of certain Pyrenomycetes, but unknown in the Discomycetes, and secondly, the fact that many species placed in the Patellariaceae cannot be distinguished from species placed by lichenologists in the family Lecidiaceae of the Cyclocarpineae.

Historical Review: Fries established the genus *Patellaria* in 1822, placing it in his division Elvelaceae, suborder Cupulati. He divided the genus into two tribes, Subcoriaceae with four species, including *P. atrata*, and Subgelatinosae with three species, including *P. pulla*. The genus was characterized as follows: "Receptaculum marginatum, patellaeforme, semper apertum, epidermide contigua. Hymenium laeve, subpersistens; sed ex ascorum dissolutione pulverulentum. Asci connati absque paraphysibus. Cupula centro affixa, passim stipitata, libere evoluta (non erumpens), planiuscula. Velum nullum. Substantia lenta, subcoriacea, raro subgelatinose." In 1825 he placed the genus in a tribe of the same name, Patellarei, in the order Phacidiacei in the Pyrenomycetes. In 1849 (16) he made the Patellariaceae one of six orders in his new group the Discomycetes, and included the following genera: *Cenangium*, *Heterosphaeria*, *Lachnella*, *Patellaria*, *Sphinctrina* and *Laquearia*.

As more detailed studies of the Discomycetes progressed, a concept of the family Patellariaceae was gradually formed by mycologists based on these essential characters: apothecia superficial,

sessile, carbonaceous or coriaceous, black, glabrous, patelliform and marginate, or rarely elliptic; spores varying from one celled and hyaline to muriform and colored; paraphyses usually enlarged and colored above, forming a heavy epithecium. Included in the family were fungi growing as saprophytes on dead wood, and many that grow as parasites on lichen thalli.

Saccardo (39) at first included nine genera in the family and later (43) increased this number to thirty-three. His classification was based on spore septation. Rehm (35) divided the family into two groups, the Pseudopatellariae with three genera, *Patellea*, *Durella* and *Caldesia*, characterized by a thin excipulum and narrow hypothecium, and the Eupatellariae with seventeen genera including both saprophytes and lichen parasites distinguished by their thick excipulums and wide hypotheciums. He also included the Calicieae and Arthonieae as an "appendix" to this family, a classification not followed by any later workers. Lindau (24) followed Rehm's classification, including twenty-one genera, Boudier (4) included thirty genera, which were placed in his inoperculate group. Ramsbottom (34) treated twenty genera, and Clements and Shear (8) include thirty-five. Keissler (21) has described eleven genera of lichen parasites in this family.

Unfortunately, most of the species of this family are seldom collected, and many of them are known only from the original type specimens. Thus our knowledge of the group has been limited to the study of herbarium material and nothing is known of the complete life history or sexual stages of these fungi. Tulasne (48) figured pycnidial stages for *Scutula epiblastematica* and *Abrothallus microspermus*. Brefeld (5) reported the formation of conidia in cultures from ascospores of *Patellea pseudosanguinea* and of *Patellea commutata*, but his cultures of *Biatorella resinae*, *Karschia lignyota* and *Patellaria proxima* remained sterile. Lohman (26) cultured *Hysteropatella Prostii* and *H. clavispora* and found the pycnidial stages of the *Hysterographium* type.

Relationships: Although this family has been placed by mycologists in the order Pezizales, its close relationship to the lichens has long been recognized. Fries emphasized the great similarity between his genus *Patellaria* and the lichen genus *Lecidea*. Rehm pointed out that the Lecidiaceae may be distinguished from the

Patellariaceae only by the presence of algae. Lindau, recognizing this close relationship, noted that we often find lichens and fungi in the same genus. Schneider (45) believed that most of the lichen genera of the family Lecidiaceae were derived from different fungal ancestors in the Patellariaceae. A. L. Smith (46) says: "There is no doubt that the Cyclocarpineae derive from some simple forms of discomycetes in the Patellariaceae. The relationship between that family and the lower Lecideae is very close. A number of fungus genera in the Patellariaceae correspond to lichen genera in the Lecidiaceae." Clements and Shear believe that the main line of evolution of the lichens sprang from this family, and they further state (8): "It is practically certain that a considerable number of natural genera are artificially divided into lichen and non-lichen groups." They have placed several genera in both the Patellariaceae and in a lichen family. For example, *Biatorella* is also included in the Lecidiaceae, and *Melaspilea* in the Graphidaceae. Fink placed the Patellariaceae in the Pezizales saying that certain species of *Patellea*, *Patinella*, *Karschia*, *Leciographa* and *Biatorella* are lichens.

Recent investigations of the genera of the Patellariaceae formerly considered as fungi growing parasitically upon lichen hosts, have shown that they are provided with gonidia and may live as parasites, parasymbionts and finally as saprophytes on the underlying substratum (22, 44). These border-line genera have always been objects of controversy, the lichenologists treating them as true lichens, the mycologists as fungi in the Patellariaceae.

It is impossible to review here all the recent literature which has led most mycologists and lichenologists to the belief that lichens are fungi, and should be classified with the fungi. According to Fink's definition (14): "A lichen is a fungus which lives during all or part of its life in parasitic relation with an algal host and also sustains a relation with an organic or an inorganic substratum." The difficult problem of reclassifying the fungi to include the lichens, has so far been met only by interpolating large groups of lichens between the orders of fungi to which they seem most closely related. Fink (12) placed the lichens of the Cyclocarpineae in the order Lecanorales after the Pezizales, but said they cannot be more closely combined until more is known of the

complete life histories of many forms in both groups. Nannfeldt (30, p. 62) pointed out several distinguishing characters between the discolichens of the Lecanorales and the Pezizales. Aside from the difference in the habit of nutrition, the apothecia of the fungi in the Lecanorales are of longer duration than the Pezizales, the hyphae have a peculiar cartilaginous consistency, isolechenin is formed by most of them, the asci are thick walled, and the paraphyses form a heavy epithecium. He believed that many of the so-called "transition forms" in the Patellariaceae belong in the order Lecanorales.

This taxonomic study of the North American species of the Patellariaceae has revealed no characters by which many of the genera of the Patellariaceae can be separated from corresponding genera in the Lecidiaceae. I believe these genera should be combined. In structure of the apothecia, asci and spores, they show close relationship with the Phacidiaceae, Tryblidiaceae, and Hysteriaceae, as well as with the Lecidiaceae. The separation of many genera in these families has undoubtedly been artificial, but their true relationships can only be determined when sufficient comparative data of their complete life histories is available.

The discovery (6) of a type of dehiscence in *Lecanidion atratum*, that is typical of certain Pyrenomycetes, or the Ascoloculares according to Nannfeldt, has added one more complicating factor to the study of the natural affinities of this group. It has already been pointed out that the method of ascus dehiscence is considered a reliable criterion upon which to base large group relationships. It has not been possible so far to determine the method of ascus dehiscence for all the genera that have been included in the Patellariaceae. However, it is certain that some of them (for example *Patellea*, *Durella* and *Patinella*) do not have this type of dehiscence, and therefore should not be classified with *Lecanidion atratum*. It is extremely interesting that Nannfeldt, on the basis of different characters, had already separated these genera into other families in his order Helotiales. On the other hand, there are many genera which have been placed in other families, for example *Tryblidiella* in the Tryblidiaceae, which have the endo-ascus type of dehiscence and probably are more closely related with *Lecanidion atratum*. This type of dehiscence may form the basis

for a new and more natural classification of the Patellariaceae, Phacidiaceae and Tryblidiaceae.

METHODS

These descriptions and drawings were made from dried herbarium material. The apothecia were softened with water, embedded in agar, and sectioned with a freezing microtome. For study of different stages of ascus development, crushed apothecia were mounted in lactophenol with added acid fuchsin and cotton blue (27). The iodine test was applied, but generally found unreliable in this material. Measurements of asci and spores were made from the longest and widest parts. Average measurements are given and strikingly different single exceptions are placed in parentheses. The "apex" of a spore is the end lying toward the apex of the ascus, as the spores are arranged within the ascus. Drawings were made with the aid of a camera lucida. The asci and spores of all the species in each genus were drawn at the same magnification, but a higher magnification was used for genera with small spores.

In the citation of herbarium specimens examined, the following abbreviations are used:

A = New York State Museum, Albany; B = Botanisches Museum der Universität, Berlin; B.M. = British Museum of Natural History, London; Br = Jardin Botanique de l'Etat, Brussels; E = Royal Botanic Garden, Edinburgh; F = Farlow Herbarium, Harvard University; G = Herbar Boissier and Institut de botanique systematique de l'Université, Geneva; K = Royal Botanic Gardens, Kew; L = Persoon Herbarium, Leiden; N. Y. = New York Botanical Garden; P = Museum National d'Histoire Naturelle, Paris; St = Naturhistoriska Riksmuseum, Stockholm; U = Fries Herbarium, Uppsala; V = Naturhistorischen Museum, Vienna; W = Herbarium of the U. S. Dept. of Agr., Washington.

THE GENUS LECANIDION

LECANIDION Endl. Fl. Poson. 46. 1830.¹

Patellaria Fries, Syst. Myc. 2: 158. 1822. Not *Patellaria* Hoffm. Pl. Lich. 1: 54. 1791.

Patella Chev. Fl. Envir. Paris 1: 302. 1826.

Cycledum Wallr. Fl. Crypt. Germ. 2: 511. 1833.

¹ This genus is not to be confused with *Lecanidium* Massal., which according to Zahlbruckner is a synonym of *Pertusaria*.

Apothecia perennial and persistent, changing little upon drying, occurring scattered or gregarious upon dead wood or herbaceous stems, superficial, sessile, dark brown or black, carbonaceous, becoming soft when moist, orbicular, oblong or elliptic when young, typically patelliform and marginate when mature, the disk plane and smooth; the excipulum well developed, composed of parallel rows of hyphae, the outermost layers with thickened, dark colored walls; the wide hypothecium colorless, or colored somewhat lighter than the excipulum; asci cyindric or clavate, the wall thickened at the apex, 4-8 spored; the spores ejected forcefully from the tip of an endoascus, the ectoascus rolling back in the form of a wrinkled ring; spores 3 to many septate, spindle or club-shaped, often curved, typically biseriate, hyaline and filled with oil droplets, frequently germinating within the ascus; paraphyses numerous, branched, septate, with enlarged colored tips closely agglutinated forming a heavy epithecium² above the asci.

The history of the generic name *Patellaria* is a complicated one, and particularly confusing as the name has been referred to different plants by mycologists and lichenologists.

The name *Patellaria* was first used by Ehrhart in 1789 as a name for *Lichen upsaliensis* L. in a list of "nomia usalia." According to Barnhart (3), these were not generic names proposed by Ehrhart, but a list of single names to be used alone without generic names, and they are untenable. Hoffman (19) in 1791, crediting Ehrhart with suggesting the name, validly published the generic name *Patellaria* for a group of lichens including the scutelliform lichens of Linnaeus and the crustaceous lichens of Michelli. Thirty-six species were placed in the genus, about half of which Hoffman himself later divided into several genera.

Persoon (32) adopted the name *Patellaria* placing the genus in the family Scutellis and including two species, both of which Hoffman later placed in the genus *Verrucaria*. Acharius (2) used *Patellaria* as a tribe of crustaceous lichens. Five years later he (1) established the genus *Lecidea* and many of Hoffman's species of *Patellaria* were placed in the section Catillaria of the genus *Lecidea*. The remaining species of *Patellaria* were divided among several different genera and the name *Patellaria* was not retained

² The term "epithecium" is used here as defined by Clements and Shear (8, p. 442), not in the sense of the lichenologists (14) for a structureless thalloid remnant lying upon the hymenium.

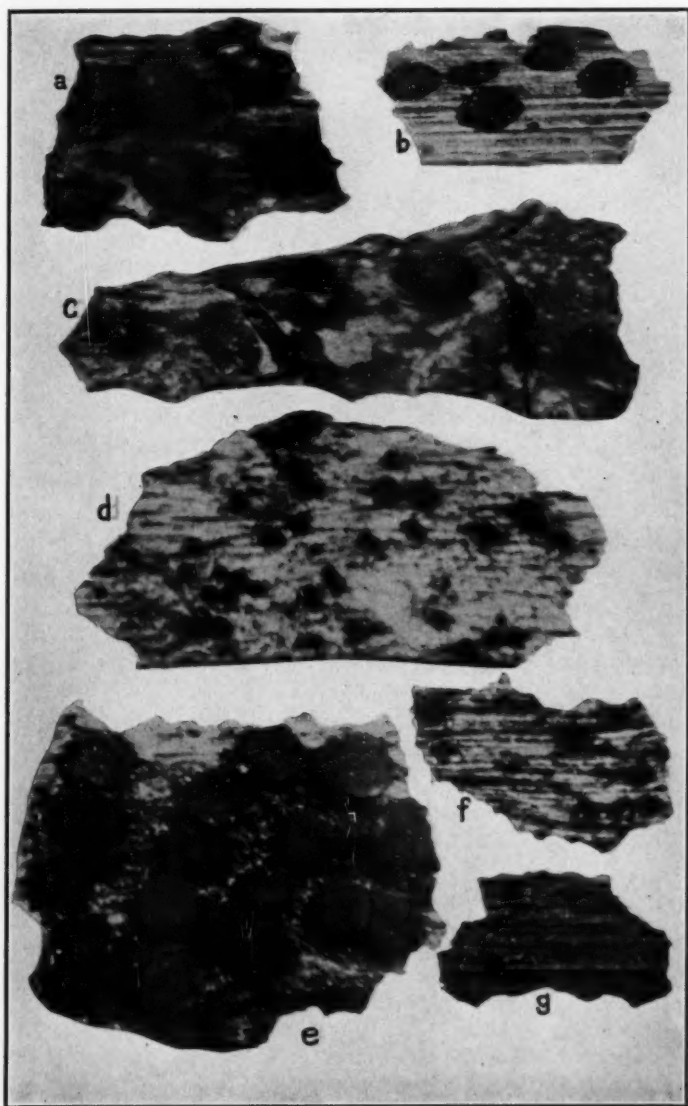


FIG. 1. Enlarged photographs of apothecia: a, *Lecanidion simile*; b, *L. atratum*; c, *L. clavisporum*; d, *L. pusillum*; e, *Karschia stygia*; f, *K. lignyota*; g, *K. imperfecta*.

for any of them. Since that time *Patellaria* has had a most fluctuating history as a lichen genus, having been completely dropped by many and retained usually in a still different sense by others.

DeCandolle (7) revived *Patellaria* Hoffm. in a modified sense. Leman (23) followed deCandolle, criticizing Acharius for not retaining the name for one of his sections—when he originally divided Hoffman's *Patellaria*. Müller Argeau (29) also used *Patellaria* in the sense of deCandolle. In 1890 Wainio (49) reduced *Patellaria* to synonymy and this course has been followed by all later lichenologists, including A. L. Smith and Zahlbruckner.

The greatest confusion came about when the name appeared in mycological literature for a genus of the cup-fungi, closely related to the lichens, established by Fries in 1822. In 1825 Fries (18) designated *Patellaria atrata*, with colorless septate spores, as the type of the genus *Patellaria* in the order Phacidiaeci of the Pyrenomycetes. In 1828 he (15) divided the genus in two parts, the first typified by *P. atrata* he placed in the Pyrenomycetes, the second typified by *P. pulla* in the Trémellei.

According to the International Rules of Nomenclature, *Patellaria* Fries is not valid, as the name had been previously used. In 1830 Endlicher proposed the name *Lecanidion* for *Patellaria* Fries, including only the species *L. atratum*, so that it is clearly the type. Rabenhorst (33) followed Endlicher, making *Patellaria* Fries a synonym of *Lecanidion*. He is often erroneously credited with having proposed the name *Lecanidion*. Saccardo (39) accepted the name *Lecanidion* Endl., but retained the name "*Patellaria* Hedw. emend." in an entirely new sense for species with colored spores! Boudier (4) also used *Patellaria* Wahl. for species with colored septate spores. This is invalid. The name *Patellaria* can not be used for any of these fungi, and *Patellaria* Fries becomes a synonym of *Lecanidion* Endl.

KEY TO THE SPECIES OF LECANIDION

Asci with eight spores.

Apothecia with a black margin.

Paraphyses enlarged above.

Tips of paraphyses colored dark blue.

1. *L. atratum*.

Tips of paraphyses bead-like and colored brown.

2. *L. clavisporum*.

- Paraphyses not enlarged above. 3. *L. pusillum*.
 Apothecia with a prominent fuscous margin. 4. *L. simile*.
 Asci with four spores. 5. *L. tetrasporum*.

1. *LECANIDION ATRATUM* (Hedw.) Endl. Fl. Poson. 46. 1830.

Lichen atratus Hedw. Descr. Musc. Frond. 2: 61. 1789.

Peziza patellaria Pers. Syn. Fung. 670. 1801.

Peziza atrata Wahlb. Flor. Ups. 465. 1820. Not *Peziza atrata*
 Pers. Syn. Fung. 669. 1801.

Patellaria atrata Fries, Syst. Myc. 2: 160. 1822.

Patella biformis Chev.³ Fl. Gen. Envir. Paris 1: 302. 1826.

Patellaria Verbasci Schw. Trans. Am. Phil. Soc. II. 4: 236.
 1832.

Cycledum atrum Wallr. Fl. Crypt. Germ. 2: 511. 1833.

Patellaria socialis De-Not. in Giorn. Bot. Ital. 2: 232. 1846.

Patellaria culmigena De-Not. in Giorn. Bot. Ital. 2: 232. 1846.

Opegrapha Lecanactis Massal. Symm. Lich. 64. 1855.

Ucographa atrata Massal. Symm. Lich. 64. 1855.

Patellaria concolor Fries, Hoffm. Ic. An. Fung. 99. 1865.

Pragmophora Lecanactis Koerb. Parerg. Lichen. 279. 1865.

Patellaria indigotica Cooke & Peck, Ann. Rep. N. Y. State Mus.
 25: 98. 1873.

Patellaria cyanea Cooke, Jour. Linn. Soc. 17: 142. 1880.

Durella atrata Rehm, Ascom. Lojk. 18. 1882.

Durella atrella Rehm, Ascom. Lojk. 18. 1882.

Durella socialis Sacc. Syll. Fung. 8: 791. 1889.

Lecanidion concolor Sacc. Syll. Fung. 8: 796. 1889.

Lecanidion indigoticum Sacc. Syll. Fung. 8: 797. 1889.

Lecanidion cyaneum Sacc. Syll. Fung. 8: 801. 1889.

Patellaria atrata f. *indigotica* Rehm, Ann. Myc. 4: 337. 1906.

Patellaria Henningsii Ranojevie, Ann. Myc. 8: 354. 1910.

Lecanidion Henningsii Sacc. & Trott. Syll. Fung. 22: 756. 1913.

Apothecia scattered or usually thickly gregarious (FIG. 1b), at first slightly sunken and closed, globose or hysteriform, at maturity expanded, superficial, sessile, typically patelliform or occasionally elliptical, with an elevated margin, reaching a diameter of from

³ This is indexed as *Patellaria biformis*. Fries in Elench. Fung. 2: 15. 1828 cites *P. difformis* Chev. as a synonym of *Patellaria atrata*, a mistake in spelling copied later by others.

0.5–1.7 mm.; black, smooth, carbonaceous when dry, subgelatinous when moist, disc smooth, plane or slightly convex; excipulum 20–40 μ thick, composed of close parallel septate hyphae, the inner periclinal hyphae thick walled and hyaline, the outermost rows with thick brown-black walls; hypothecium 50–80 μ wide, the cells just below the hymenium with thin hyaline walls, those of the basal part elongated and with dark thickened walls (FIG. 2A); asci clavate (FIG. 4), short stipitate, rounded above with the wall thickened at the apex, reaching a length of from 70–157 μ and a diameter of 15–20 μ (average length 90–122 μ), 8 spored; spores irregularly biseriate, clavate, with the apex blunt and gradually tapering below, often slightly curved, hyaline, 5–11 septate, the cells usually containing 1 or more oil drops, 20–50 μ long by 6–12 μ wide (average length 30–45 μ). Paraphyses numerous, filiform, septate, branched above with the tips enlarged to 4–6 μ wide and colored dark blue, rarely olive-brown, extending above the asci and closely agglutinated forming a thick epithecium.

On a wide variety of woody and herbaceous stems, old rugs, old paper and sacking.

TYPE LOCALITY: Europe.

DISTRIBUTION: Throughout Europe, North America, Mexico, Bermuda and Hawaii.

SPECIMENS EXAMINED: *Anderson*, Parasitic Fungi of Montana, 571 (N. Y.); *Anzi*, Lich. rar. Veneti 96 (K, N. Y., St, V); *Ayer*, on *Salix* (K); *Baker*, C. F., Pacific Slope Fungi 179 (B, P, N. Y., V); *Bartholomew*, Kansas Fungi 485 (N. Y.); 943 (N. Y.); 1046 (N. Y.); Flora of Kansas, March 20, 1896 (St); *Berkeley*, 80 (K); 336 (K); 3350 (K); *Bethel*, Colorado 330 (N. Y.); *Bisby*, 1649 (N. Y.); *Bisby*, *Buller & Hanna*, 4651 (N. Y.); *Bisby & Gordon*, 4650 (N. Y.); *Blake*, 130 (N. Y.); *Bloxam*, "Gallo Provincio" (B. M.); *Boudier*, Abbe Gretes (P); *Brenckle*, Fungi Dak. 586 (N. Y.); 665 (N. Y.); 698 (St); South Dakota Fungi 1766 (N. Y.); *Brongniart*, "Lichen atratus" (P); *Brown*, *Britton & Seaver*, Bermuda 19 (N. Y.); 22 (N. Y.); 1223 (N. Y.); 1466 (N. Y.); *Caldesi*, Erb. Critt. Ital. II. 821 (Br, G); *Cavara*, Fung. Longobard. 167 (B, B. M., N. Y., V, W); *Cooke*, 27 (Ed); 350 (K); Fungi Brit. Exs. 194 (Ed, K); *Cummins*, 98 (N. Y.); 98a (N. Y.); 99 (N. Y.); 100 (N. Y.); 144 (N. Y.); 172 (N. Y.); *Dearness*, 3413 (St); *Desmazieres*, Plantae Crypt. de France I. 429 (B. M., G, K, N. Y.); 41 (P); *Earle*, F. S., Flora of Alabama 151 (N. Y.); *Earle*, F. S. & *Baker*, C. F., Alabama Biol. Surv. 1/23 '97 (N. Y.); *Earle*, F. S. & *Earle*, *Esther S.*, Plants of New Mexico, Lincoln Co. 7/26. 1900 (N. Y.); *Earle*, F. S. & *Underwood*, L. M., Flora of Alabama, Feb. 15, 1896 (N. Y.); *Ellis*, N. Am. Fungi 64 (A, Br, B. M., K, N. Y.); 893 (N. Y.); 1061 (N. Y.); 1258 (N. Y.); *Ellis & Everhart*, Fungi Columb. 746 (B. M., G, N. Y.); N. Am. Fungi 2051 (B. M., Br, F, K, N. Y.); *Fairman*, 14 (St); 1904 (A); *Farlow*, 395 (F, N. Y.); 1167 (B, N. Y.);

Fautrey, Herb. Crypt. de la Cote D'Or 395 (P); *Ferry*, 531 (P); *Finl.*, Ascomycetes of Ohio, col. by Bachman 7/31. 1907 (N. Y.); *Flowtow*, Lich. Exs. 257 (B); *Fries*, Lund (U); *Fuckel*, Enum. Fung. Nass. 765 (N. Y.); *Fungi Rhenani* 1118 (B. M., Br, F, G, K, N. Y., V); *Gerard*, N. Am. Fungi 1069 (B. M., N. Y.); *Harkness*, 2670 (B. M.); 2944 (B. M.); 2993 (B. M.); *Hokway*, 352 (N. Y.); *Johnson*, 1563 (N. Y.); *Kellerman & Swingle*, 1414 (N. Y.); *Koerber*, Lich. Sel. Germ. 199 (G, N. Y., St); *Kunze*, Flora von Eisleben 533 (B); 1875 (St); *Langlois*, Flora Ludoviciana 271 (F, N. Y.); 1290 (N. Y.); 1638 (N. Y.); 2231 (N. Y.); *Linabed*, in Herb. E. Fries (U); *Lowe*, 172 (N. Y.); *Morgan*, 24 (N. Y.); 61 (N. Y.); 276 (N. Y.); 278 (N. Y.); 279 (N. Y.); 663 (N. Y.); 893 (N. Y.); *Nees*, Lugd. Bot. 910, 261-363 (L); *Passerini*, Erb. Critt. Ital. 1172 (G, V); *Paris Herb.*, on *Ribes*, Torino (P) Type of *P. socialis*; *Peck*, 117 (N. Y.); *Savannah* (A, N. Y., K) Type of *P. indigotica*; *Persoon Herb.*, Lugd. Bot. 910, 261-342 (L); 910, 261-360 (L); 910, 261-361 (L); 910, 256-338 (L); *Petrak*, Fl. Boh. & Mor. Exs. 272 (Br, E, N. Y.); *Phillips*, Elv. Brit. 90 (E, K, N. Y., W); *Piskor*, Flora Moravica IV. 1935 (N. Y.); *Pringle*, 1167 (N. Y.); *Rabenhorst*, Fungi Eur. 1612 (B, B. M., Br, G, K, N. Y., St, V); *Ranojevic*, 154. 1906 (St) Type of *P. Henningsii*; 302 (B); *Ravenel*, 223 (B. M., K, N. Y.) Type of *P. cyanea*; 518 (B. M.); 1445 (K, N. Y.); 1640 (B. M., K); *Rehm*, Ascomyceten 574 (B, Br, K, N. Y.); *Lojka* 51 (St); *Lojka* 194 (St); III. 1910 (St); *Roumeguère*, Fungi Gallici Exs. 828 (Br, G, K, N. Y.); *Fungi Sel. Exs.* 5526 (B, G, K, N. Y.); *Saccardo*, Myc. It. 1676 (N. Y., W); *Myc. Ven.* 263 (B. M., K, N. Y., St, V, W); 791 (P); *Treviso* (K, N. Y.); *Schwcinitz Herb.* (K, N. Y., U) Type of *P. Verbasci*; *Seaver*, Iowa Fungi 108a (N. Y., St); 108b (N. Y.); *Seaver & Bethel*, Fungi of Colorado 1910 (N. Y.); *Shear*, Lincoln, Nebraska on *Ulmus* (W); 5903 (W); *Smith, A. H. & Cummins*, 100 (N. Y.); *Sydow*, Myc. Germ. 2719 (E, K); *Myc. Mar.* 4757 (B. M., N. Y.); *Thaxter*, R. 107 (N. Y.); *Tulasne Herb.*, St. Cloud (P); *Underwood*, 52 (N. Y.); *Waterston*, 238 (N. Y.); *Winter Herb.*, Fungi Hungarici—113 (St, V); *Woronow*, Fungi Caucasici 199 (St, N. Y.); *Zwack*, Lich. 444 (N. Y.).

This species was designated by Fries (18) as the type of the genus *Patellaria*. Specimens of Fries, Fung. Sclerom. Suec. no. 336 labeled *Patellaria atrata*, examined at Kew and Berlin do not conform to his description, and were named *Tympanis confusa* by Nylander (31). However, a specimen in the Fries Herbarium at Uppsala, collected in Lund, agrees in all respects with Fries' description of *Patellaria atrata*. This specimen is identical with four specimens in the Persoon Herbarium at Leiden, labeled *Peziza Patellaria*, and may be considered as authentic type material of this species. Fries (17) cites *Peziza Patellaria* Pers. as a synonym of *Patellaria atrata*. There are five other specimens in the Persoon Herbarium also labeled *Peziza Patellaria* which do not belong in the genus *Lecanidion*.

Patellaria indigotica Cooke & Peck was distinguished by the bluish tint of the hymenium, and as that color is also typical of *Lecanidion atratum*, and the type material agrees in all other respects with the latter, they are considered synonymous.

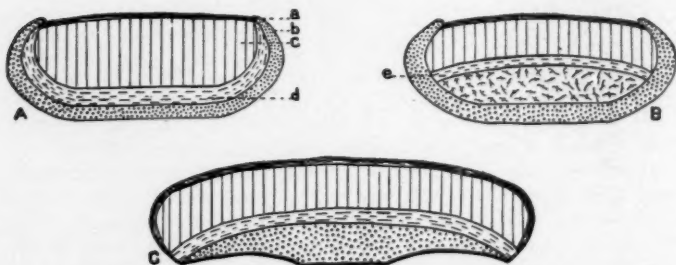


FIG. 2. Diagrams of sections through mature apothecia: A, *Lecanidion atratum*, a, epithecium, b, excipulum, c, hymenium, d, hypothecium; B, *Lecanidion simile*, e, region of hypothecium containing calcium oxalate crystals; C, *Karschia stygia*.

Patellaria cyanea Cooke was described as having spores 3–5 septate, but a study of type material showed that the spores may become 5–7 septate and it is identical with *Lecanidion atratum*.

A specimen of *Patellaria socialis* De-Not. apparently from the type collection, examined in the Paris Herbarium, agrees in all characters with *Lecanidion atratum*. The asci and spores are large, becoming 11 septate. This makes a wide range in ascus and spore size in *Lecanidion atratum*, but no other differences can be found for separating either the small spored or large spored types.

No material of *Patellaria concolor* Fries in Hoffm. has been available for study, but it is placed in synonymy here on the basis of Hoffman's description and illustration.

Specimens of *Patellaria Verbasci* Schw. from the Schweinitz Herbarium were examined at Kew, Uppsala, and The New York Botanical Garden. It is the same as *Lecanidion atratum*.

DeNotaris distributed material under the name *Patellaria culmigena* De-Not., and later wrote (10) that he considered it the same as *Patellaria atrata*. A specimen of *Patellaria culmigena* De-Not. examined in the Paris Herbarium is *Lecanidion atratum*.

A specimen of *Patellaria Henningsii* Ran. on *Verbascum*, collected in Belgrade, apparently from the type collection, was examined in the Sydow Herbarium at Stockholm. It is identical with *Lecanidion atratum*.

The apothecia of this fungus are persistent, and were reported by Fries as perennial. It is not unusual to find germinating spores in the asci.

Lecanidion atratum has been described as a lichen with a thallus in the genera *Plagmopara*, *Ucographa* and *Opegrapha*. In the hundreds of specimens examined no thallus was found, although the apothecia occurring on wood are frequently closely associated with algae.

Curry (9) reported a second type of fructification; smaller plants without asci, the hymenium composed of a mass of clavate, septate spores, which he believed may be related to *Lecanidion atratum*. An asexual stage has not been more definitely reported for this species.

2. *LECANIDION CLAVISPORUM* (Berk. & Br.) Sacc. Syll. Fung. 18: 184. 1906.

Patellaria clavispora Berk. & Br. Ann. Mag. Nat. Hist. II. 13: 456. 1854. Not *Patellaria clavispora* (Peck) Sacc.

Patellaria Crataegi Phillips, Grevillea 17: 46. 1888.

Durella clavispora Sacc. Syll. Fung. 8: 794. 1889.

Lecanidion Crataegi Sacc. Syll. Fung. 8: 799. 1889.

Patellaria corticola Starb. Bih. K. Svensk. Vet. Akad. Handb. 21^a: 23. 1895.

Lecanidion corticolum Sacc. & Sydow, Syll. Fung. 14: 821. 1899.

Apothecia erumpent or superficial from the beginning (FIG. 1c), sessile, subglobose at first, expanding at maturity, patelliform or somewhat irregular in shape, reaching a diameter of 0.5–2 mm., marginate, black, carbonaceous when dry, soft when moist and brown in color, white within, disc plane or slightly concave; excipulum about 80 μ thick, composed of closely interwoven hyphae with the walls thickened and dark brown, and arranged in parallel rows at the surface; hypothecium hyaline, brownish beneath gradually grading into the excipulum; asci cylindric-clavate with the wall slightly thickened at the rounded apex and staining blue with

iodine (FIG. 6), gradually tapering beneath to a slender stipe, reaching a length of from 90–160 μ and a diameter of 8–13 μ , 8 spored; spores biseriate above, uniseriate below, narrowly clavate-fusiform with the apex rounded and tapering below to the acute base, straight or slightly curved, hyaline, 3–5 (6) septate, 21–36 (60) μ long and 5–6 μ wide; paraphyses numerous, slender, septate, branched, enlarged above and colored brown with the irregularly nodulose tips (moniliform) closely adhering, forming a brown epithecium.

On *Crataegus*, *Fagus grandifolia*, *Ligustrum* and *Quercus*.

TYPE LOCALITY: Lucknam, Wiltshire, England.

DISTRIBUTION: Canada, England, Sweden, Switzerland.

SPECIMENS EXAMINED: *Berkeley*, on Privet, Lucknam, Nov. 4, 1852 (K) Type of *P. clavisporea*; *Bloxam*, 86 (K); *Cooke*, Capron (E); Oct. 1856 (K); Ann 774 (K); Cliff House (K); *Currey*, Benthall Hill, Oct. 1856 (K); Sept. 1862 (K); *Eliasson*, 27 (St. N. Y.) Type of *P. corticola*; *Jackson*, Crypt. Herb. Univ. Toronto 2861 (N. Y.); *Massee*, Twycross (N. Y.); *Phillips*, 3 Corbie Den 1/2/87 (B. M.) Type of *P. Crataegi*; *Romell*, 1/7.1887 (K, N. Y.).

There has been a great deal of confusion in this country as to the correct identification of *Lecanidion clavisporum*. This was due to the wide distribution in the Ellis and Morgan collections of specimens of *Lecanidion atratum* with asci and spores somewhat smaller than the average, incorrectly labeled *Patellaria clavisporea*. This misidentification was the basis of Morgan's statement (28): "This species (*P. clavisporea*) is commonly confused with *P. atrata*" and led to the general belief here that *Patellaria clavisporea* is a synonym of *Lecanidion atratum*. The type specimen of *Lecanidion clavisporum* was studied in the Berkeley Herbarium at Kew and found to be a distinct species. It may easily be distinguished from *Lecanidion atratum* and *L. simile* by its brown moniliform paraphyses aptly described by Berkeley and Broome as follows: "Paraphyses branched, bearing at their tips one or more dark bodies sometimes arranged like the joints of a necklace." The paraphyses are so striking in structure that Currey (9, p. 227) believed they bore conidia, describing them thus: "The brown colour is entirely owing to the small brown stylospores or conidia which are attached to the tips of the paraphyses and which bear some resemblance to the spores of a *Cladosporium*."

The type specimen of *Patellaria Crataegi* Phillips was examined in the Phillips Herbarium at the British Museum and, although the asci and spores were somewhat larger than is typical for *Lecanidion clavisporum*, this was not considered of sufficient importance to keep the two species separate. An examination of material from the type collection (Eliasson no. 27) of *Patellaria corticola* in Rehm's Herbarium at Stockholm, and at The New York Botanical Garden, showed it to be identical with *Lecanidion clavisporum*.

It is unfortunate that fresh material of this species has not been available for study. Nannfeldt (30) considered it unrelated to *Lecanidion atratum*, but was uncertain where to place it. It is retained here, in the genus *Lecanidion*, until the type of ascus dehiscence is known and sufficient comparative data regarding the complete life history of these forms is available, so that its natural affinities may be determined.

3. *LECANIDION PUSILLUM* (Peck) Sacc. Syll. Fung. 8: 799. 1889.

Patellaria pusilla Peck, Bull. N. Y. State Mus. Nat. Hist. 12: 22. 1887.

Apothecia globose at first, later expanding and becoming patelli-form with a narrow regular margin (FIG. 1d), reaching a diameter of from 0.5–0.8 mm., black, carbonaceous when dry, gelatinous when moist with the disc appearing a dirty gray, disc smooth, plane or slightly convex when moist; excipulum 22–39 μ thick composed of parallel rows of elongated cells with slightly thickened light brown walls; hypothecium about 66 μ wide colored a light brown; asci clavate (FIG. 5), gradually tapering below, rounded above with the wall slightly thickened at the apex, reaching a length of 59–82 μ and a diameter of 8–12 μ , not staining blue with iodine; spores irregularly crowded or biseriate, lanceolate or sub-clavate, 5–7 septate, 12–17 μ long by 2–4 μ wide; paraphyses numerous, filiform, not enlarged above.

On beech wood.

TYPE LOCALITY: Catskill Mountains, New York.

DISTRIBUTION: This species is apparently known only from the type collection in New York State.

SPECIMENS EXAMINED: Peck, 18 Catskill Mountains, N. Y. (A, N. Y.) Type.

The ascospores in this species give rise to hundreds of small spores, as in the genus *Tympanis*. This character is considered by most mycologists as a difference of generic significance. It is not possible, on the basis of the scanty herbarium material available for study, to ascertain any more closely the natural relationships of *Lecanidion pusillum*, and the species is retained here for the present.

4. *Lecanidion simile* (Gerard) E. T. Butler, comb. nov.

Patellaria similis Gerard, Bull. Torrey Club 5: 26. 1874.

Patellaria atrofusca Berk. & Curt. Grevillea 4: 2. 1875.

Cenangium concinnum Berk. & Curt. Grevillea 4: 5. 1875.

Patellaria oleosa Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26. 1877.

Patellaria fusco-atra Rehm in Ellis, N. Am. Fungi 447. 1880.

Lecanidion fuscoatrum Rehm; Sacc. Michelia 2: 141. 1880.

Durella fuscoatra Rehm, Ber. Nat. Ver. Augsburg 26: 113. 1881.

Scleroderis concinna Sacc. Syll. Fung. 8: 595. 1889.

Durella similis Sacc. Syll. Fung. 8: 794. 1889.

Lecanidion atrofusum Sacc. Syll. Fung. 8: 800. 1889.

Apothecia superficial, sessile (FIG. 1a), at first orbicular with a prominent fuscous margin, later expanding and becoming patelliform, margin persistent, reaching a diameter of 0.5–1 mm., carbonaceous and shiny when dry, becoming gelatinous when moist, disc smooth, black, brown when moist, plane or slightly convex, chalky white within; excipulum 35–52 μ thick, composed of parallel rows of closely interwoven hyphae with thickened brown walls; hypothecium thick, 208–230 μ wide, the region just below the hymenium (26–39 μ wide) composed of hyphae colored a bright orange yellow, below that a hyaline region (182–195 μ wide) where the hyphae are completely covered by calcium oxalate crystals which give the characteristic chalky white appearance to the broken apothecia (FIG. 2B); asci cylindric-clavate (FIG. 7), short stipitate, the wall thickened and staining deep blue with iodine at the rounded apex, reaching a length of 59.5–132 μ and a diameter of 10–14 μ , 8 spored; spores irregularly crowded or biseriate above, uniseriate below, or rarely uniseriate throughout, fusiform-elliptical, straight or slightly curved, triseptate or rarely four-septate, hyaline, 14–22 μ long by 3–4 μ wide; paraphyses numerous, filiform, septate, branched and slightly wider above, encrusted with a brown substance, extending above the asci and closely agglutinated forming a heavy brown epithecium.

On *Carya*, *Cercis*, *Laurus*, *Ligustrum*, *Quercus* and *Vitis*.

TYPE LOCALITY: Poughkeepsie, New York.

DISTRIBUTION: Alabama, Delaware, Mississippi, Missouri, New Jersey, South Carolina, Virginia.

SPECIMENS EXAMINED: *Berkeley*, 2460 (K, N. Y.); *Commons*, 2126 (N. Y.); *Demetrio*, 49 (N. Y.); *Earle & Baker*, 2256 (N. Y.); Alabama Biol. Surv. on *Vitis rotundifolia* 3/21. 1897 (N. Y.); *Ellis*, N. Am. Fungi 447 (B, B. M., K, N. Y.); 106a (N. Y.); *Ellis & Everhart*, Fungi Columb. 1226 (B. M., G, N. Y.); *Gerard*, on *Quercus rubra*, Poughkeepsie (K, N. Y.) Type of *P. similis*; *Morgan*, 1226 (N. Y.); *Peters*, 5238 (K) Cotype of *C. concinnum*; *Ravenel*, Fung. Am. Exs. 313 (B. M., K, N. Y.); 1678 (B, M., K, N. Y.) Type of *P. oleosa*; 2210 (F, K) Type of *P. atrofusca*; 2295, 3828, 6172 (K) Cotypes of *C. concinnum*; 2358 (B. M., K, N. Y.); *Rehm*, Ascomyceten 464 (B, B. M., F, K, N. Y., St) Type of *L. fuscoatrum*.

The apothecia of this species may be readily distinguished by the fuscous color beneath which extends up into the margin, and in cross section by the wide hypothecium containing calcium oxalate crystals, as well as by the asci and spores. The broken bases of old apothecia, having a characteristic chalky appearance are frequently persistent.

The number of the type species of *Patellaria atrofusca* Berk. & Curt. is mistakenly printed in the original description as Car. Inf. 3210. The number is 2210 on the type specimen which was examined in the Berkeley Herbarium at Kew and found to be identical with *Patellaria similis* Gerard. None of the material examined showed the character, "springing from a black thin stratum which surrounds the twigs" as described by Berkeley and Curtis.

Abundant type material of *Patellaria fuscoatra* Rehm (Ascom. 464) from Newfield, N. J., has been available for study and agrees in all respects with the type specimen of Gerard's species. The four cotypes of *Cenangium concinnum* and the type (Ravenel 1678) of *Patellaria oleosa* were examined at Kew and found to be identical with *Patellaria similis*. It is interesting to note that a specimen of Ravenel 1678 in the Ellis Collection at The New York Botanical Garden is labeled *Patellaria fuscoatra* in Ellis' handwriting, and Saccardo (40) cites this number as *L. fuscoatrum*.

Patellaria purpurea Petch is very similar to this species in ex-

ternal appearance, and the tip of the ascus stains blue, but it may be distinguished by its larger, long stipitate asci (reaching a length of 160μ), and larger, uniseriate spores.

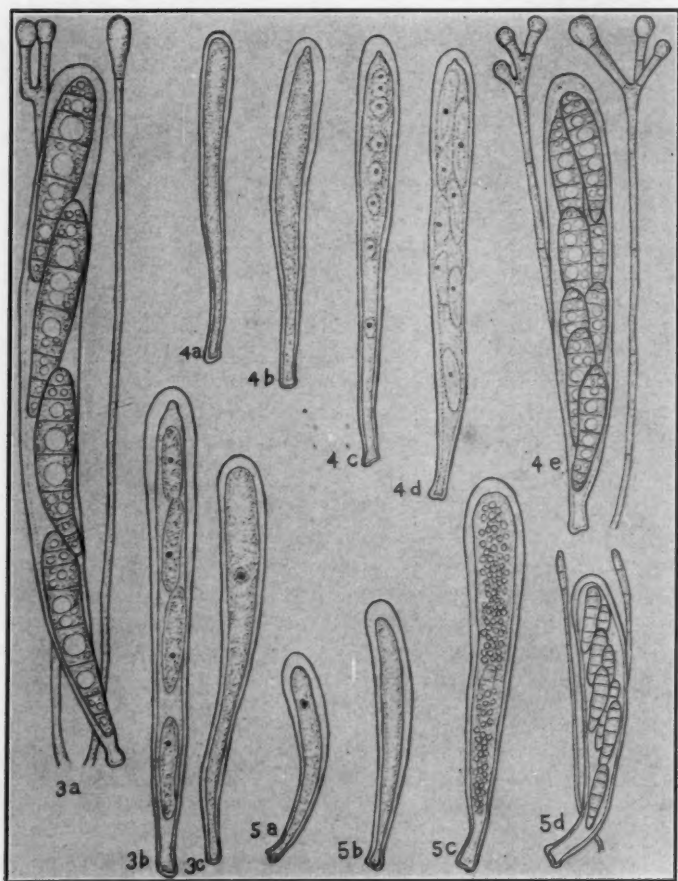


FIG. 3a. Paraphyses and mature ascus with spores of *Lecanidion tetrasporum*; b, c, younger stages in the development of the ascus. FIG. 4a-d. Development of the ascus of *L. atratum*; e, paraphyses and mature ascus with spores of *L. atratum*. FIG. 5a, b. Development of the ascus of *L. pusillum*; c, older ascus containing many small spores; d, paraphyses and mature ascus with spores.

5. *LECANIDION TETRASPORUM* (Massee & Morgan) Seaver, Proc. Iowa Acad. Sci. 12: 118. 1905.

Patellaria tetraspora Massee & Morgan, Jour. Myc. 8: 180. 1902.

Apothecia usually gregarious, occasionally scattered, superficial, ellipsoid at first with the margin vertically striate, expanding and at maturity reaching a diameter of 0.5–1 mm., patelliform with a persistent margin, black, smooth, carbonaceous, and somewhat gelatinous when moist, disc smooth and plane; excipulum and hypothecium similar to *Lecanidion atratum*; asci cylindric (FIG. 3), abruptly narrowed below into a short and slender stipe, rounded above with the wall slightly thickened at the apex, varying in length from 125–190 μ and in diameter from 12–14 μ (average length 140–160 μ), 4 spored; spores uniseriate, clavate, with the apex blunt and the base acute, 6–9 septate, the cells containing 1 or more large conspicuous oil drops, 38–70 μ long by 10–11 μ wide (average length 40–50 μ); paraphyses numerous, slender, septate and branched above with the thickened tips colored a deep blue and closely agglutinated forming a heavy blue epithecium above the asci.

On *Acer saccharinum*, *Aralia spinosa*, *Juglans cinerea*, *Ulmus*.

TYPE LOCALITY: Preston, Ohio.

DISTRIBUTION: Alabama, Connecticut, Iowa, Louisiana, Massachusetts, Michigan, New York, Ohio, West Virginia, Wisconsin and Canada.

SPECIMENS EXAMINED: *Baker*, 395 (N. Y.); *Berkeley Herb.*, 936 (K); *Cook*, O. F., 140 (N. Y.); *Cummins*, 101 (N. Y.); 103 (N. Y.); *Curtis*, 1378 (P); *Dearness*, 1088 (N. Y.); *Earle & Baker*, Alabama Biol. Surv. on old stump 1/23/97 (N. Y.); *Ellis*, 1004 (N. Y.); *Fairman*, Lyndonville, N. Y. Oct. 188– (N. Y.); *Farlow Herb.*, Lincoln, Mass. on oak, April 2, 1899 (F); *Langlois*, 271 (N. Y.); *Massee & Morgan*, 31 (N. Y.); *Morgan*, 25 (N. Y.) Type; 60 (N. Y.); 264 (N. Y.); *Nuttall*, Flora of Fayette Co., W. Va. 359 (N. Y.); *Seaver*, Iowa Fungi, Nov. 6, 1905 (N. Y.).

This species was formerly reported only from Iowa and Ohio. In going through collections of North American Patellariaceae, numerous specimens of *L. tetrasporum* were found incorrectly identified as *P. atrata* or *P. indigotica*. This was probably due to their close resemblance in external appearance and the similar bluish color of the paraphyses. *L. tetrasporum* is distinguished from *L. atratum* by the narrower cylindric asci which contain four

uniserial spores. As the four spored condition is constant, apothecia never having both 8 spored and 4 spored asci, it is retained as a distinct species.

The statement by Massee & Morgan (28) that *Patellaria tetraspora* is allied to *Patellaria clavispora* Berk. & Br. is undoubtedly accounted for by Morgan's misconception of the true identity of *P. clavispora*. (See the discussion under *L. clavisporum*.)

DOUBTFUL AND EXCLUDED SPECIES

- Patellaria abietina* Cooke, Grevillea 7: 4. 1878. = *Patinella abietina* (Cooke) Sacc. Syll. Fung. 8: 771. 1889.
- Patellaria acericola* Atk. in herb. Albany. (*Lecanidium acericolum* Atk. in Peck, Ann. Rep. N. Y. State Bot. 49: 24. 1896. = *Dermatea acerina* (Peck) Rehm, Ber. Bayer. Bot. Ges. 13: 197. 1912.
- Patellaria agyrioides* Rehm, Hedwigia 39: 322. 1900. No material of this species has been seen but according to von Höhnelt, Sitzb. K. Akad. Wiss. Wien, Math. Nat. Kl. Abt. 1, 127: 558. 1918, it belongs in the genus *Melittosporium* Corda.
- Patellaria applanata* Berk. & Curt. Jour. Linn. Soc. 14: 108. 1875. = *Catinella nigroolivacea* (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.
- Patellaria atrovinosa* Blox. in Berk. & Br. Ann. Mag. Nat. Hist. III. 15: 447. 1865. = *Durella atrovinosa* (Blox.) Sacc. Syll. Fung. 8: 794. 1889.
- Patellaria aureococcinea* Berk. & Curt. in Ellis, N. Am. Fungi I. no. 63. 1878. = *Solenopeziza aureococcinea* (Berk. & Curt.) Rehm, Ann. Myc. 2: 352. 1904.
- Patellaria californica* Rehm, Ann. Myc. 9: 367. 1911. No material of this species has been available for study.
- Patellaria carolinensis* Ellis & Ev. Jour. Myc. 1: 152. 1885. = *Scutularia carolinensis* (Ellis & Ev.) Sacc. Syll. Fung. 8: 808. 1889.
- Patellaria carpinea* (Pers.) Berk in herb. Berk. at Kew. = *Pezicula carpinea* (Pers.) Tul. Sel. Fung. Carp. 3: 183. 1865.
- Patellaria cenangicola* Ellis & Ev. Jour. Myc. 4: 56. 1888. = *Godroniopsis querneae* (Schw.) Diehl & Cash, Mycologia 21: 244. 1929.
- Patellaria clavata* Ellis, Bull. Torrey Club 8: 74. 1881. = *Belonidium clavatum* (Ellis) Rehm, Ann. Myc. 2: 354. 1904.
- Patellaria clavispora* (Peck) Sacc. Syll. Fung. 8: 787. 1889. = *Hysteropatella clavispora* Seaver, Bull. Lab. Nat. Hist. State Univ. Iowa 6: 113. 1910. This is a homonym and must be renamed.
- Patellaria congregata* Berk. & Curt. in Massee, Jour. Linn. Soc. 35: 109. 1901. = *Durella compressa* Tul. Sel. Fung. Carp. 3: 177. 1865.
- Patellaria convivens* Fries, Summa Veg. Scand. 366. 1845. = *Durella convivens* Rehm, Ber. Nat. Ver. Augsburg. 26: 9. 1881.
- Patellaria constipata* Berk. in Cooke, Handb. Brit. Fung. 720. 1871. = *Pezicula livida* (Berk. & Br.) Boud. Disc. Eur. 159. 1907.
- Patellaria cucurbitaria* Rehm, Ascom. 311. 1875. = *Blitrydium Cucurbitaria* (Cooke) Sacc. Syll. Fung. 8: 804. 1889.

- Patellaria cyanea* Ellis & Martin, Jour. Myc. 1: 97. 1885. = *Patellea cyanea* Sacc. Syll. Fung. 8: 784. 1889. This is a homonym and must be re-named.
- Patellaria cylindrospora* Ellis, Bull. Torrey Club 6: 108. 1876. = *Scutularia cylindrospora* Sacc. Syll. Fung. 8: 808. 1889.
- Patellaria difformis* Lambotte, Flore Myc. Belg. 275. 1880. = *Biatorella difformis* (Fries) Rehm in Rab. Krypt.-Fl. 3: 306. 1895.
- Patellaria dispersa* Gerard, Bull. Torrey Club 5: 26. 1874. This species belongs in the genus *Blitrydium*.
- Patellaria fenestrata* Cooke & Peck, Ann. Rep. N. Y. State Mus. 28: 68. 1879. = *Blitrydium fenestratum* Sacc. Syll. Fung. 8: 805. 1889.
- Patellaria ferruginea* Cooke & Ellis, Grevillea 5: 91. 1877 [as *fuliginosa* Sacc. Syll. Fung. 8: 787. 1889]. = *Dermatea ferruginea* Rehm, Ann. Myc. 2: 353. 1904.
- Patellaria flexella* (Ach.) Phill. Brit. Disc. 362. 1887. = *Lithographa flexella* (Ach.) Zahlb. in E. & P. Nat. Pfl. 1: 93. 1903.
- Patellaria gnaphaliana* Cooke & Ellis, Grevillea 6: 92. 1878. = *Pyrenopeziza gnaphaliana* Rehm, Ann. Myc. 2: 354. 1904.
- Patellaria Hamamelidis* Peck, Ann. Rep. N. Y. State Mus. 33: 32. 1880. = *Dermatella Hamamelidis* Durand, Bull. Torrey Club 29: 464. 1902.
- Patellaria hirneola* Berk. & Br. Jour. Linn. Soc. 14: 108. 1875. = *Catinella nigroolivacea* (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.
- Patellaria Hyperici* Phill. Grevillea 10: 69. 1881. = *Durella atrocyanea* Höhnelt, Ann. Myc. 16: 210. 1918.
- Patellaria inclusa* (Pers.) Karst. Myc. Fenn. 1: 236. 1871. = *Odontotrema inclusum* Karst. Rev. 146. 1885.
- Patellaria Lecideola* Fries, Summa Veg. Scand. 366. 1845. = *Durella Lecideola* Rehm, Ascom. Lojke. 19. 1882.
- Patellaria leptosperma* Peck, Ann. Rep. N. Y. State Mus. 30: 62. 1878. = *Holwaya gigantea* (Peck) Durand, Bull. Torrey Club 28: 354. 1901.
- Patellaria leucochaetes* Ellis & Ev. Jour. Myc. 1: 152. 1885. = *Scutularia leucochaetes* Sacc. Syll. Fung. 8: 809. 1889.
- Patellaria livida* Berk. & Br. Ann. Mag. Nat. Hist. 13²: 466. 1854. = *Pezicula livida* (Berk. & Br.) Boud. Disc. Eur. 159. 1907.
- Patellaria Lonicerae* Phill. Brit. Disc. 364. 1887. = *Durella vilis* Starb. Bih. Svensk Vet. Akad. Handb. 21²: 22. 1895.
- Patellaria lurida* Berk. & Curt. in Phill. Grevillea 19: 75. 1891. = *Phacidium luridum* (Berk. & Curt.) Phill. Grevillea 19: 75. 1891.
- Patellaria melaleuca* Fries, Summa Veg. Scand. 366. 1845. = *Mollisia melaleuca* Sacc. Syll. Fung. 8: 337. 1889.
- Patellaria melaxantha* Fries, Summa Veg. Scand. 366. 1845. = *Blitrydium melaxanthum* Sacc. Syll. Fung. 8: 806. 1889.
- Patellaria minor* Karst. Myc. Fenn. 1: 233. 1871. = *Odontotrema minus* Nyl. Lich. Scand. 249. 1861.
- Patellaria nigrocinnabarina* Schw. Trans. Am. Phil. Soc. II, 4: 236. 1832. = *Rhytidopeziza nigrocinnabarina* Sacc. Syll. Fung. 10: 65. 1892.
- Patellaria nigrocyanea* Phill. & Hark. Bull. Calif. Acad. Sci. 1: 24. 1884. = *Durella nigrocyanea* Sacc. Syll. Fung. 8: 793. 1889.
- Patellaria nigroolivacea* Fries in Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26.

1877. = *Catinella nigroolivacea* (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.
- Patellaria nigrovirens* Sacc. & Ellis, *Michelia* 2: 572. 1880. This species belongs in the genus *Leciographa*.
- Patellaria olivacea* (Batsch) Phill. Brit. Discom. 361. 1887. = *Catinella nigroolivacea* (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.
- Patellaria olivaceovirens* (Schw.) Fries, *Syst. Myc.* 2: 159. 1822. A fragmentary specimen of this species examined at Kew was a lichen.
- Patellaria Peckii* House, Bull. N. Y. State Mus. 22: 233. 1921. = *Hysteropatella clavisporea* Seaver, Bull. Lab. Nat. Hist. State Univ. Iowa 6: 113. 1910.
- Patellaria proxima* Berk. & Br. Ann. Mag. Nat. Hist. 7^o: 450. 1861. = *Durella atrocyanea* (Fries) Höhnelt, Ann. Myc. 16: 211. 1918.
- Patellaria pulla nigroolivacea* Fries, *Syst. Myc.* 2: 160. 1822. = *Catinella nigroolivacea* (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.
- Patellaria Ravenelii* (Berk. & Curt.) Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26. 1877. The specimens examined were sterile.
- Patellaria recisa* Berk. & Curt. in Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 27. 1877. = *Gorgoniceps Guernisaci* Sacc. Syll. Fung. 8: 505. 1889.
- Patellaria rhabarbarina* Berk. Grevillea 4: 2. 1875. = *Pezicula rhabarbarina* (Berk.) Tul. Sel. Fung. Carp. 3: 183. 1865.
- Patellaria Rhododendri* Schw. Trans. Am. Phil. Soc. II. 4: 236. 1832. No material has been available for study.
- Patellaria Rubi* Libert, Pl. Ard. 231. 1834. = *Pezicula rhabarbarina* (Berk.) Tul. Sel. Fung. Carp. 3: 183. 1865.
- Patellaria signata* Ellis & Ev. Washington Lab. Nat. Hist. 1: 4. 1884. = *Blitrydium signatum* Sacc. Syll. Fung. 8: 807. 1889.
- Patellaria sphaerospora* Berk. & Curt. in Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26. 1877. = *Lagerheima sphaerospora* Sacc. Syll. Fung. 10: 55. 1892.
- Patellaria subsidua* Cooke & Ellis, Grevillea 6: 8. 1878. = *Blitrydium subsiduum* Sacc. Syll. Fung. 8: 805. 1889.
- Patellaria subsecta* Cooke in Phill. Brit. Discom. 365. 1887. = *Durella atrocyanea* (Fries) Höhnelt, Ann. Myc. 16: 211. 1918.
- Patellaria subvelata* Ellis & Ev. Jour. Myc. 1: 152. 1885. This is a species of *Arthonia*.
- Patellaria triseptata* (Karst.) Sacc. Syll. Fung. 8: 787. 1889. = *Leciographa triseptata* Morgan, Jour. Myc. 8: 180. 1902.
- Patellaria tuberculosa* Ellis, Bull. Torrey Club 8: 74. 1881. = *Belonidium clavatum* (Ellis) Rehm, Ann. Myc. 2: 354. 1904. The types of *P. tuberculosa* and *B. clavatum* were examined in the Ellis Collection at The New York Botanical Garden. Both species occur on old stems and leaves of *Andropogon*, and are identical.
- Patellaria violacea* Berk. & Br. Jour. Linn. Soc. 14: 108. 1875. = *Catinella nigroolivacea* (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.
- Patellaria viticola* Pers. Myc. Eur. 1: 309. 1822. No specimens were available for study.

THE GENUS KARSCHIA

KARSCHIA Koerb. Parerg. Lich. 459. 1865.

Poetschia Koerb. Parerg. Lich. 280. 1861.

Karschiella Sacc. Syll. Fung. 18: 177. 1908.

Epilichen Clements, Gen. Fung. 69. 1909.

Buelliella Fink, Lich. Fl. U. S. 372. 1935.

Apothecia scattered on dead wood or lichen thalli, superficial, globose when young, becoming patelliform at maturity and usually immarginate, disc flat or convex when moist, black, coriaceous or carbonaceous, softening when moist; excipulum pseudoparenchymatous composed of dark walled spherical or hexagonal cells; hypothecium thick and usually colored; asci clavate, with the wall thickened at the rounded apex, 8 spored; spores clavate, oblong or elliptic, two-celled, usually with one or more oil drops in each cell, becoming brown; paraphyses septate, branched, colored at the tips and closely agglutinated with extraneous material forming a heavy colored epithecium.

Karschia is one of the most interesting genera on that confusing border line between the lichens and the fungi. It has been placed in the Patellariaceae by most workers, but was considered by Nannfeldt (30, p. 65) as a group reduced from the Physciaceae.

The fungi placed in this genus grow either as saprophytes on wood or as parasites on other lichens. Saccardo suggested the subgenus *Karschiella* for those forms parasitic on lichens, and Clements made a new genus, *Epilichen*, for the parasitic species. Fungi with apothecia agreeing in structure with *Karschia*, but with a definite or evanescent thallus, are placed in the lichen genus *Buellia*. Fink proposed the new genus *Buelliella* for the species of *Buellia* that grow as parasites on other lichens. There are no morphological characters for separating these genera. This raises the difficult question of basing generic divisions entirely on physiological differences. A number of species are known as "facultative lichens," for they may live part of the time without gonidia, as saprophytic fungi. Reinke (38) has reported this condition for *Buellia myriocarpa*. Tobler (47) says that *Karschia destructans* grows as a parasymbiont on the thallus of *Chaenotheca chyrscephala*, penetrates through the thallus living as a parasite on the algae and finally lives as a saprophyte on the bark beneath. When

a single plant has these varied methods of nutrition in its life cycle, one immediately sees the fallacy of separating genera on that distinction alone. For in this case one would be faced with the ridiculous situation of calling the fungus *Epilichen* at first, then *Buellia*, and finally *Karschia*. I believe that these genera should all be combined. *Buellia* is the oldest name and by the rule of priority will be used for the group. According to Fink (12) *Buellia* belongs in the Lecidiaceae in his order Lecanorales. A. L. Smith (46, p. 341) and Zahlbruckner make a separate family for *Buellia* and *Rinodina*, the Buelliaceae, closely allied to the Physiaceae. Only the North American species of *Karschia* are discussed here. A study of the genus *Buellia* has been started, and the genera will be combined as quickly as possible.

KEY TO THE SPECIES OF KARSCHIA

Apothecia attached by a central point.

Excipulum composed of large hexagonal cells.

1. *K. stygia*.

Apothecia not attached by a central point.

Hymenium yellow-green in section.

Spores "slipper shape."

2. *K. lignyota*.

Hymenium colorless in section.

Spores elliptic-cylindric.

3. *K. imperfecta*.

1. *KARSCHIA* STYGIA (Berk. & Curt.) Masee, Jour. Linn. Soc. 35: 107. 1901.

Patellaria stygia Berk. & Curt. Grevillea 4: 2. 1875.

Patellaria nigerrima Sacc. Atti Soc. Veneto Sci. Nat. Padova IV. 1: 29. 1875.

Patellaria fusispora Cooke & Peck, Ann. Rep. N. Y. State Mus. 28: 67. 1876.

Patellaria Bloxami Berk. in Phill. Brit. Disc. 361. 1887.

Karschia fusispora Sacc. Syll. Fung. 8: 781. 1889.

Patellaria stygia Sacc. Syll. Fung. 8: 783. 1889.

Karschia Bloxami Sacc. Syll. Fung. 8: 781. 1889.

Karschia nigerrima Sacc. Syll. Fung. 8: 780. 1889.

Karschia Taveliana Rehm in Rab. Krypt.-Fl. 1^o: 1223. 1896.

? *Karschia elaeospora* Fairman, Proc. Rochester Acad. Sci. 6: 105. 1921.

Apothecia scattered or sometimes crowded (FIG. 1e), superficial, at first orbicular with a narrow margin, expanding at maturity to

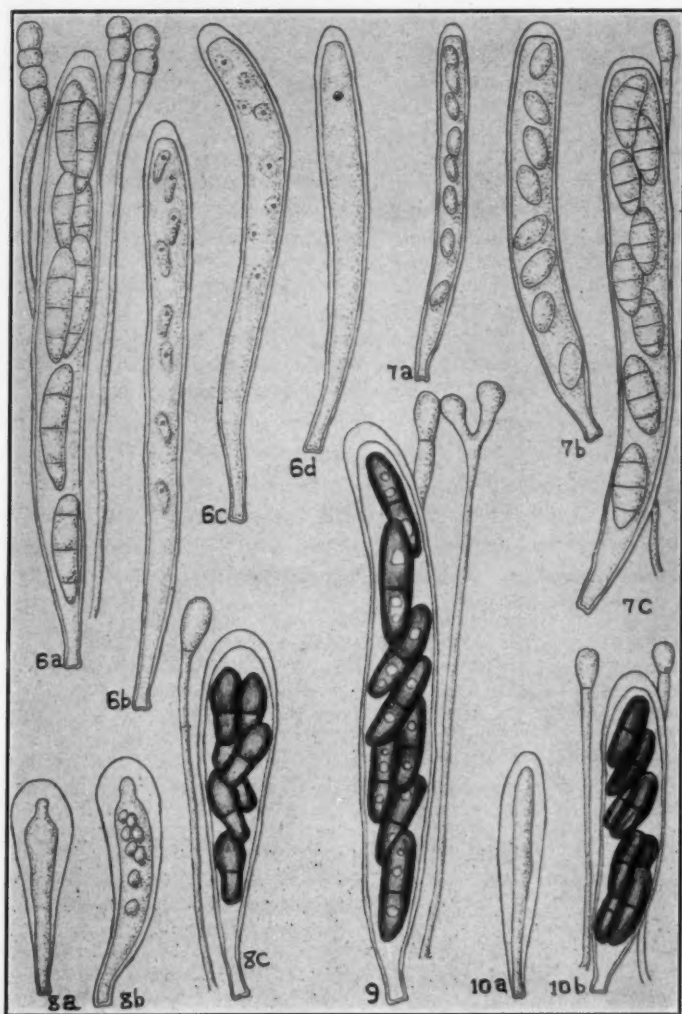


FIG. 6a. Paraphyses and mature ascus with spores of *L. clavisorum*; b-d, younger stages in ascus development. FIG. 7a, b. Development of the ascus of *L. simile*; c, paraphyses and mature ascus with spores. FIG. 8a, b. Development of the ascus of *Karschia lignyota*; c, paraphyses and mature ascus with spores. FIG. 9. Paraphyses and mature ascus of *K. stygia*. FIG. 10a. Young ascus of *K. imperfecta*; b, paraphyses and mature ascus with spores.

a diameter of 0.5–2 mm., round or slightly contorted by mutual pressure, immarginate, attached by a central point, shiny black, fuscous beneath, glabrous, carbonaceous, disc plane, becoming strongly convex and softened when moist; excipulum pseudoparenchymatous, composed of large hexagonal cells 15–33 μ in diameter, those toward the outside with thick, brown walls; hypothecium red-brown, about 50 μ wide, composed of small cells with thick red-brown walls, arranged parallel with the surface of the hymenium, and grading gradually into the excipulum (FIG. 2C); asci cylindric-clavate (FIG. 9), the wall thickened at the slightly narrowed apex, reaching a length of 50–75 (99) μ and a diameter of 6–10 μ , 8 spored; spores irregularly biseriate, elliptic-subcylindric, often a little curved, guttulate, light brown, 15–20 μ long by 4–6 μ wide; paraphyses numerous, filiform, branched and septate, enlarged above, tips colorless or brown, closely agglutinated with a brown extraneous substance forming a brown epithecium.

On *Aleurites*, *Alnus*, *Carpinus*, *Liriodendron*, *Populus* and *Tilia*.

TYPE LOCALITY: New Jersey and South Carolina.

DISTRIBUTION: Georgia, Indiana, Iowa, Massachusetts, Michigan, New Jersey, New York, Ohio, South Carolina, Virginia; Canada; Bermuda; Mexico; England; Germany; Italy.

SPECIMENS EXAMINED: *Bloxam*, Sept. 17, 1856 (K); *Twycross* (K) Type of *P. Bloxami*; *Brown*, *Britton & Seaver*, Expl. Bermuda 1488 (N. Y.); *Cavara*, Fung. Longobardiae 116 (B, B. M., L, N. Y., V, W); *Davidson*, 733b (W); *Dearnness*, 1097 (N. Y.); *Fairman*, Myc. Fairman 4528 (Cornell) Type of *K. elaeospora*; *Fink*, Porto Rican Fungi 2057 (N. Y.); 2057 (N. Y.); *Fink & Fuson*, Ascom. Ind. 188 (H); *Gerard*, 11 (N. Y.); *Holway*, 333 (N. Y.); *Kauffman*, 1910, Ann Arbor (N. Y.); *Macoun*, 405 (N. Y.); *Kew Herb.*, N. J. 4590 (K, N. Y.) Cotype of *K. stygia*; *Massee*, N. J. 4500 (N. Y.); *Morgan*, 7 (N. Y.); 260 (N. Y.); 266 (N. Y.); 905 (N. Y.); *Murrill*, *W. A. & E. L.*, Fungi Tepite Valley 524 (N. Y.); 457 (N. Y.); *Peck*, Portville, N. Y. 1059 (A, K, N. Y.) Type of *P. fusispora*; 133 (K); *Rabenhorst*, Fung. Eur. 1152 (B, Br, G, K, N. Y., V); *Ravenel*, Car. Inf. 3911 (K) Cotype of *K. stygia*; *Saccardo*, Myc. Ven. 1201 (K, N. Y.); *Treviso* (B, K) Type of *K. nigerrima*; *Schweinitz* Herb., "Patellaria difformis" (K); *Seaver*, Iowa Fungi 87a (N. Y.); *Shimek*, 43 (N. Y.); *Thaxter*, Farlow Herb. 1023 (H); 670 (H); *Thompson*, Univ. Toronto Herb. 2058 (N. Y.).

The three specimens reported by Berkeley and Curtis in the original description of the species, were examined in the herbarium at Kew and are considered type material. One of them (Sprague 6234) is not *K. stygia* but is *K. lignyota*. The other two (Ravenel 3911 and New Jersey 4590) agree with the type description.

Specimens of *K. nigerrima* Sacc. from the type collection on *Alnus* in Treviso were examined at Kew and Berlin, and found to be identical with *K. stygia*. The type of *K. fusispora* was examined in Peck's Herbarium at Albany and it agrees in all respects with *K. stygia*. No specimen of *K. Taveliana* Rehm could be found in Rehm's Herbarium in Stockholm, but material in The New York Botanical Garden Herbarium collected by Seaver in Iowa and identified by Rehm as *K. Taveliana* is the same as *K. stygia*. This is considered sufficient evidence, since Rehm's original description of the species is also in perfect agreement with *K. stygia*, to place the species in synonymy here. The type of *P. Bloxami* Berk. in Berkeley's Herbarium at Kew was examined, and although the spores seem more broadly elliptical than is typical of *K. stygia*, as it was the same in all other characters, it is considered a synonym of *K. stygia*.

Karschia elaeospora Fairman is apparently known only from the original collections. The type specimen was sent to me for examination from the herbarium of Cornell University through the courtesy of W. L. White. The material is extremely fragmentary. It seems to be the same as *K. stygia*, although the two apothecia that appear mature are small, and the spores are shorter, averaging only 13μ in length. The red-brown hypothecium and large celled excipulum are typical of *K. stygia*.

This species is easily distinguished by the large apothecia, attached at a central point, and in section by the red-brown hypothecium and the conspicuous, hexagonal cells of the excipulum.

2. *KARSCHIA LIGNYOTA* (Fries) Sacc. Syll. Fung. 8: 779. 1889.
Peziza (Patellea) lignyota Fries, Syst. Myc. 2: 150. 1822.
Patellaria lignyota Fries, Summa Veg. Scand. 366. 1849.
Arthonia melaspermella Nyl. Flora 48: 605. 1865.
Karschia Strickeri Koerb. Parerg. Lich. 460. 1865.
Patellaria Strickeri Sacc. Michelia 1: 57. 1879.
Poetschia Strickeri Stein in Cohn Krypt.-Fl. Schles. II. 2: 224. 1879.
Karschia nigricans Rehm, Ber. Nat. Ver. Augsburg 26: 10. 1881.

Karschia sphaerioides Ellis & Ev. Proc. Acad. Phil. 453. 1893.

Apothecia scattered or slightly crowded (FIG. 1f), superficial, globose, at first with a conspicuous incurved irregular margin, expanding to a diameter of 0.3–1 mm., typically patelliform with the margin almost disappearing when mature, flat and sessile, brown-black when young, becoming black with age, smooth, cartilaginous, softening when moist, disc plane; excipulum about $10\ \mu$ wide, pseudoparenchymatous, composed of hyphae with thick brown walls; hypothecium about $50\ \mu$ wide, yellow-brown in color, gradually grading into dark brown pseudoparenchyma at the base, with numerous brown-black hyphae spreading from the base into the substratum; asci broadly clavate (FIG. 8), with the wall greatly thickened at the rounded apex, tapering beneath to a short stipe, reaching a length of 25–45 (55) μ and a diameter of 10–14 μ , 8 spored; spores irregularly arranged, ovate-oblong, 2 celled, slightly constricted at the septum, the upper cell a little wider than the lower, blunt or slightly narrowed at the apex giving a characteristic slipper shape, with a large oil drop in each cell, 8–12 (16) μ long by 4–5 μ wide; paraphyses numerous, filiform, branched above, septate, the enlarged tips colored brown and closely agglutinated forming a heavy epithecium above the asci.

On *Abies*, *Acer*, *Betula*, *Carpinus*, *Hypoxylon*, *Nyssa*, *Ostrya*, *Quercus*, *Ulmus*; *Polyporus*; thalli of *Biatorina pineti* and *Microphiale diluta*.

TYPE LOCALITY: Europe.

DISTRIBUTION: Alabama, Florida, Michigan, New Hampshire, New Jersey, New York; England; Germany; Italy; Switzerland.

SPECIMENS EXAMINED: *Commons*, 1338 (N. Y.); *Earle*, Alabama Biol. Surv. 12/10/99 (N. Y.); *Ellis*, N. Am. Fungi 400 (A, B, M., H, K, N. Y.); 1064 (N. Y.); 3022 (K, N. Y.); *Newfield*, N. J. March 26, 1893 (N. Y.) Type of *Karschia sphaerioides*; *Farlow*, Chocorua, N. H. Sept. 28, 1907 (H, N. Y.); *Holway*, 364 (N. Y.); *Morgan*, 33 (N. Y.); *Phillips*, Elv. Brit. 146 (B, E, K, N. Y.); *Plowright*, 1064 (N. Y.); *Ravenel*, Car. Inf. 1224 (K); *Rehm*, Ascom. 21 (K, N. Y., V); *Roumeguère*, Fung. Sel. Exs. 7350 (G, N. Y.); *Smith*, H. & A., 6197 (N. Y.); *Sprague*, 6234 (K); *Wehmeyer*, 212 (N. Y.).

This species is readily distinguished by the characteristic yellow green color of the hymenium in section, and by the slipper shape of the spores. An examination of the type specimen of *K. sphaerioides* Ellis & Ev. showed that it is identical with *K. lignyota*. The margins of the apothecia are no more strongly incurved than is typical for *K. lignyota*.

It is interesting to note that mycologists and lichenologists have disagreed as to the classification of *K. lignyota*. As Currey said: "It is a doubtful plant, which seems to hover between the fungi and lichens." Lindsay (25) said: "It has equal claim to be considered a lichen or fungus." Nylander placed it with the lichens, while Rehm considered it a fungus. As it occurs either as a saprophyte on wood or as a parasite on lichens, Keissler (21, p. 201) considered it a facultative lichen parasite.

3. *KARSCHIA IMPERFECTA* (Ellis) Sacc. Syll. Fung. 8: 782. 1889.
Patellaria imperfecta Ellis, Bull. Torrey Club 8: 74. 1881.

Apothecia scattered (FIG. 1g), superficial, globose when young with a slight brown margin, expanding to a diameter of 0.3–0.5 mm. at maturity, orbicular, immarginate, sessile, disc plane, black, smooth, or frequently dimpled in the center, carbonaceous, becoming soft when moist and strongly convex; excipulum pseudoparenchymatous, composed of hyphae with thickened light brown walls; hypothecium about $25\ \mu$ wide, red-brown in color; asci cylindric oblong (FIG. 10), the wall thickened at the rounded apex, reaching a length of $24\text{--}39\ \mu$ and a diameter of $7\text{--}12\ \mu$, 8 spored; spores biseriate, elliptic-cylindric, 2 celled, not constricted at the septa, $8\text{--}13\ \mu$ long by $3\ \mu$ wide, red-brown in color; paraphyses filiform, septate, with enlarged brown tips united into an epithecium above the asci.

On old corn stalks.

TYPE LOCALITY: Newfield, New Jersey.

DISTRIBUTION: Known only from the type locality.

SPECIMENS EXAMINED: *Ellis*, 1057 (N. Y.) Type; on old corn stalks Oct. 1879 (N. Y.); Aug. 27, 1880 N. J. (N. Y.).

This species was collected in two successive years from the same locality. It is distinguished from *K. lignyota* by the shape of the spores, the red brown hypothecium, and paler excipulum as well as by the immarginate mature apothecia.

DOUBTFUL AND EXCLUDED SPECIES

Karschia crassa Fairman, Jour. Myc. 10: 229. 1904.

The type specimen, Fairman no. 1977, collected in Lyndonville, N. Y., was sent to me from Cornell University. It is very fragmentary, but seems to agree with *Buellia myriocarpa* (Lam. & DC.) De-Not., which

according to Zahlbruckner (50) is the same as *Buellia punctata* (Hoffm.) Massal.

Karschia impressa Ellis & Ev. Bull. Torrey Club 24: 470. 1897.

This species is known only from the original collection made by Bethel in the San Juan Mountains of Colorado, on living stems of *Symphoricarpos*. It was distributed as Bethel no. 356, and in the Morgan Collection as no. 1227. In external appearance it is very like *Karschia*, although the surface is strongly papillate, a condition not typical for this genus. In cross section the asci are found to be grouped in separate locules, not in a continuous hymenium with paraphyses. The asci are cylindric-oblong, abruptly narrowed at the base, short stipitate, 40–55 μ long by 8–14 μ wide. The spores are arranged irregularly, ovate-oblong, 2 celled, with the septum nearer the apex, colored a pale yellow-brown, 8–13 μ long by 4–5 μ wide. This fungus does not belong in the genus *Karschia*. It probably should be placed in the Dothideaceae.

Karschia occidentalis Earle in Greene, Pl. Baker. 2: 8. 1901.

A portion of the type collection on *Juniperus* from Hermosa, Colorado, was examined in the herbarium at The New York Botanical Garden. It is the same as *Buellia punctata* (Hoffm.) Massal.

Karschia patinelloides (Sacc. & Roum.) Sacc. Syll. Fung. 8: 780. 1889.

The original collection by J. Therry, as distributed in Roumeguère's Fung. Gall. Exs. 1075 is the same as *Buellia punctata* (Hoffm.) Massal.

Karschia Pertusariae Vouaux, Bull. Soc. Myc. Fr. 29: 453. 1913.

This species was known from Mexico only, but Keissler (21, p. 187) found in the herbarium at Uppsala a specimen collected in Sweden. I have seen no material of this species, but Keissler considers it a valid species. It grows on the thallus of *Pertusaria*.

Karschia Ricasoliae Vouaux, Bull. Soc. Myc. Fr. 29: 448. 1913.

A new species, growing on the thallus of *Ricasolia*, reported from Mexico. No specimens have been available for study.

Karschia Sabinae (De-Not.) Rehm, Hedwigia 21: 115. 1882.

Tryblidium sabinum De-Not. Comm. Soc. Critt. 2: 491. 1867.

In 1896 Rehm (17) placed this species in the genus *Caldesia* Trev., in the Pseudopatellariaceae. He was using the name *Caldesia* in a new and entirely different sense from that of Trevisan. The species Trevisan had included in *Caldesia* belong in *Melaspilea* or *Arthonia*. Rehm was uncertain of the relationships of *Caldesia Sabinae*, and in 1912 (37) transferred it to the Cenangiaceae. Saccardo (41) included this species in the Hysteriaceae and later (42) in the Patellariaceae. In 1918 von Höhnelt (20) made *Caldesia*, in the sense of Rehm, a synonym of *Eutrybliella* Rehm (36), and the new combination *Eutrybliella sabina* (De-Not.) Höhnelt in the Tryblidiaceae. Clements and Shear (8, p. 311) placed *Caldesia* (Trev.) Rehm em. in the Tryblidiaceae and Nannfeldt (30, p. 334) made *Caldesia* Rehm (non Trev.) a synonym of *Trybliella* in the Lecanorales.

This species was first collected in this country by C. F. Baker in Hermosa, Colorado, on *Juniperus*. The apothecia are scattered, erumpent, black, carbonaceous, globose and closed at first, then opening irregularly, usually by lobes, the margin persistent. Excipulum composed

of small dark brown heavy walled cells, the hypothecium very thick. The asci are thick walled. The spores are 2 celled, brown. These characters of the apothecia separate the species from *Karschia*. It will be interesting to check the type of ascus dehiscence in fresh material. The species is without doubt closely related to *Tryblidiella rufula*.

Karschia Trypethelii (Tuck) Keissler, Ann. Nat. Mus. Wien 41: 168. 1927.

Buellia Trypethelii Tuck. Syn. N. Am. Lich. 2: 106. 1888.

Buelliella Trypethelii Fink, Lich. Fl. U. S. 372. 1935.

Tuckerman's type for this species was a specimen growing on the thallus of *Trypethelium carolinianum*, collected in Florida by A. H. Curtis. Keissler on the basis of material collected in Florida by S. Rapp, and agreeing with the original description, transferred the species to the genus *Karschia*, saying it is closely related to *K. advenula* Zopf. Fink placed it in his genus *Buelliella*. No material has been available for study, but according to the descriptions I believe it should be called *Buellia Trypethelii* Tuck.

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BIBLIOGRAPHY

1. Acharius, E. Methodus lichenes 32. 1803.
2. —. Lichenographiae suecicae prodromus 36. 1798.
3. Barnhart, J. H. The so-called generic names of Ehrhart's *Phytopylacium*. Rhodora 22: 180-182. 1921.
4. Boudier, E. Discomycetes d'Europe 145. 1907.
5. Brefeld, O. Untersuchungen Mykologie 10: 297. 1891.
6. Butler, E. T. Ascus dehiscence in *Lecanidion atratum* and its significance. Mycologia 31: 612-623. 1939.
7. Candolle, A. P. de. Flora Française 2: 345. 1805.
8. Clements, F. E. & Shear, C. L. Genera of fungi 117. 1931.
9. Currey, F. Mycological notes. Trans. Micros. Soc. London 7: 228. pl. 11, f. 10. 1859.
10. DeNotaris, G. Giornale Botanico Italiano II. 1^a: 232. 1846.
11. Ehrhart, F. Beiträge 4: 146. 1789.
12. Fink, B. The Ascomycetes of Ohio. Bull. Ohio St. Univ. 19: 21. 1915.

13. —. The lichen flora of the United States 20. 1935.
14. —. The nature and classification of lichens. *Mycologia* 5: 117. 1913.
15. **Fries, E.** *Elenchus fungorum* 2: 15. 1828.
16. —. *Summa vegetabilium Scandinaviae* 2: 364. 1849.
17. —. *Systema mycologicum* 2: 160. 1822.
18. —. *Systema orbis vegetabilis* 113. 1825.
19. **Hoffman, G. F.** *Plantarum lichenes* 1: 54. 1791.
20. **Höhnelt, F. von.** *Fragmente zur mykologie.* Sitz.-ber. Akad. Wien 127: 563. 1918.
21. **Keissler, K.** In *Rabenhorst's Kryptogamen Flora* 8: 118. 1930.
22. **Kotte, I.** Einige neue Fälle von Nebensymbiose. *Bot. Centr.* 23: 19. 1910.
23. **Leman, D. S.** *Dictionnaire sciences naturelles* 38: 76. 1825.
24. **Lindau, G.** In *Engler & Prantl, Nat. Pfl.* 1^a: 221. 1897.
25. **Lindsay, W. L.** On *Arthonia melaspermella* Nyl. nov. sp. *Jour. Linn. Soc.* 9: 268. 1867.
26. **Lohman, M.** *Hysteriaceae: Life-histories of certain species.* *Papers Mich. Acad. Sci.* 17: 277. 1933.
27. **Maneval, W. E.** *Lactophenol preparations.* *Stain Technol.* 11: 9-11. 1936.
28. **Morgan, A. P.** The *Discomycetes* of the Miami Valley, Ohio. *Jour. Myc.* 8: 180. 1902.
29. **Müller, J.** (Müll. Arg.) *Classification des lichens* 56. 1862.
30. **Nannfeldt, J. A.** Studien über die morphologie und systematik der nicht-lichenisierten inoperculaten discomyceten. *Nova Acta Regiae Soc. Sci. Upsal.* IV. 8: 196. 1932.
31. **Nylander, W.** *Observationes Pezizas fenniae* 69. 1869.
32. **Persoon, C. H.** Einige bemerkungen über die flechten, nebst beschreibungen einiger neuen arten aus dieser familie der Aftermoose. *Usteri Neue Ann.* 1: 22. 1794.
33. **Rabenhorst, L.** *Deutschlands Kryptogamen Flora* 1: 342. 1844.
34. **Ramsbottom, J.** Some notes on the history of the classification of the *Discomycetes*. *Trans. Brit. Myc. Soc.* 4: 382. 1913.
35. **Rehm, H.** In *Rabenhorst's Kryptogamen Flora* 1^a: 289. 1896.
36. —. Revisionen der Gattungen *Tryblidiella* Sacc., *Rhytidhysterium* Speg., *Tryblidaria* Sacc., *Tryblidium* Rebent., *Tryblidiopsis* Karst. *Ann. Myc.* 2: 523. 1904.
37. —. Zur Kenntniss der *Discomyceten* Deutschlands, Deutschlands Österreichs und der Schweiz. *Bay. Bot. Ges. Ber.* 13: 191. 1912.
38. **Reinke, J.** *Abhandlung über Flechten.* *Jahrb. Wiss. Bot.* 28: 92. 1895.
39. **Saccardo, P. A.** *Conspectus generum Discomyceten.* *Bot. Centr.* 18: 252. 1884.
40. —. *Fungorum Extra-Europaeorum.* *Michelia* 2: 141. 1880.
41. —. *Sylloge fungorum* 2: 741. 1883.
42. —. *Sylloge fungorum* 8: 781. 1889.
43. **Saccardo, P. A. & Sydow, P.** *Sylloge fungorum* 14: 33. 1899.

44. **Schaechtlin, J. & Werner, R. G.** Developpement et Biologie de l'Abrothallus parmeliarum Smeft. Bull. Soc. Myc. Fr. 42: 233. 1927.
45. **Schneider, A.** Text book of general lichenology 129. 1897.
46. **Smith, A. L.** Lichens 279. 1921.
47. **Tobler, F.** Zur Biologie von Flechten und Flechtenpilzen. Jahrb. Wiss. Bot. 49: 400. 1911.
48. **Tulasne, L. R.** Mémoire sur les Lichens. Ann. Sci. Nat. III. 17: pl. 16, f. 22-26; pl. 14, f. 14-24. 1852.
49. **Wainio, E.** Étude sur la Classification naturelle et la morphologie des Lichens du Brésil 2: 10. 1890.
50. **Zahlbruckner, A.** Catalogus lichenum universalis 7: 392. 1931.

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